Understanding 'Challenger' sweet corn yield, quality and phenology responses to phosphorus

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By
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The research in this thesis examined the response of field grown 'Challenger' sweet corn crops to P supply at Lincoln Canterbury, New Zealand in 2001/02 and 2002/03. Initial soil tests showed that the site had an available soil P (Olsen, bicarbonate extraction) of 6 $\mu g\ ml^{-1}$. In both 2001/02 (0, 50, 100, 150 and 200 kg P ha^{-1}) and 2002/03 (0, 50, 110, 170 and 240 kg P ha^{-1}) five rates of P fertiliser were applied to these crops. The kernel yield and biomass responses to P were then examined. Initially, a traditional empirical approach was used to analyse the yield responses to a P fertiliser. This described the asymptotic increase of both kernel yield and crop biomass to increasing P supply. kernel yield ranged from 2.0 to 4.4 t DM ha^{-1} in response to P fertiliser. These P responses were specific to this experiment. Therefore to provide greater understanding and insight into crop growth the mechanisms of these responses were examined in detail. An adjacent experiment with 5 rates of N fertiliser (0, 45, 90, 180 and 300 kg N ha^{-1}) showed that N had only a minor impact on kernel yield of sweet corn and therefore these treatments were not studied further. Except that these data were included in a preliminary analysis of DM partitioning in response to crop DM produced.

The increased kernel yield with P fertiliser was associated with changes in total crop biomass (9.7-15.7 t ha^{-1}). However, the partitioning of this biomass was conservative with 24%

kernels, 44% stems and leaves and 32% ears. Ear quality, unfilled tip length and individual kernel mass, was also from crops with the greatest biomass. The application of P fertiliser also decreased the time from crop emergence to canning maturity by 6-7 days. This acceleration was caused by an 80-115 °Cd (T_b = 8 °C) decrease in the period from crop emergence to silking.

The causes of the differences in crop biomass were then investigated in terms of radiation interception and use. Total accumulated intercepted solar radiation (RI_{cum}) was 23 and 39% greater when 200 or 240 kg P ha^{-1} was applied in 2001/02 and 2002/03, respectively, compared with the 0 kg P ha^{-1} crops. This was due to both a faster leaf appearance rate and a greater area of each individual leaf. The phyllochron (°Cd between successive leaf tips) was 4-6 °Cd longer in the 0 kg P ha^{-1} than in the 200 and 240 kg P ha^{-1} crops in both seasons. The appearance of fully expanded leaves showed a similar pattern with a delay in the 0 kg P ha^{-1} crops compared with the crops receiving P fertiliser. The area of individual leaves followed a bell shaped curve. The largest leaf was consistently leaf 11 or 12, which was 29-37% larger when P was applied, compared with the 0 kg P ha^{-1} crops. The addition of P fertiliser had only a minor effect on the final number of mainstem leaves (16.7-18.0). P fertiliser did not affect either the rate at which the fraction of senesced leaf area increased or the extinction coefficient (0.65).

The radiation use efficiency (RUE) was consistent with a previously established temperature response and unaffected by P supply. However, during the early phases of crop growth (RI_{cum}<134 MJ m^{-2}) RUE was only ~50% of the 1.3 g DM MJ^{-1} found for the majority of the crop duration. The mechanisms responsible for this were unclear and require further examination. With the exception of the first and smallest leaves (<8), the specific leaf

phosphorus (SLP) was always greater than 0.1 g P m^{-2} and photosynthesis was unaffected by P supply. In the first leaves the SLP was less than 0.1 g P m^{-2} for the 0 kg P ha^{-1} plots and consequently there was a minor decrease in leaf photosynthesis in these crops during this phase.

The response to P supply of crop maturity, phyllochron, fully expanded leaf appearance, individual leaf area and RUE were incorporated into a simple framework for simulating yields. Combining this with long term weather data from both Hawkes Bay (1976-2002) and Lincoln (1960-2003) showed that a single yield response curve would have been inappropriate for multiple sites and seasons. Although P fertiliser had a marked effect on simulated kernel yield, the greatest source of variability in simulated yields was from seasonal weather variations. Insufficient P also increased the risk of a crop failing to mature before the first autumn frost by ~10% at Lincoln from a range of typical sowing dates. In contrast this risk was minor at Hawkes Bay.

Overall, the dominant effect of P supply on kernel yield in 'Challenger' sweet corn was on RI_{cum}, with conservative RUE and DM partitioning. Further research should aim to isolate the mechanisms by which P supply limited individual leaf areas and leaf appearance rates. These data could be linked to a mechanistic model of soil P uptake to form a powerful research tool for analysing P responses for crops in other sites and seasons.

Keywords:

development, individual leaf area, leaf appearance rates, leaf area index, modelling, nitrogen, partitioning, plastochron, photosynthesis, phyllochron, radiation interception, radiation use efficiency, thermal time, *Zea mays*.

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Abbreviations

Abbreviation	Description	Units
A	Asymptote (Equation 4.1)	t ha^{-1}
a	Intercept of Equation 5.1 with y axis	leaves
ai	Active ingredient	-
AWC	Available water holding capacity	mm
B	Reduction from asymptote with no fertiliser (Equation 4.1)	t ha^{-1}
b	Curvature of Equation 5.1	-
c	Kurtosis of Equation 2.3	-
CAN	Calcium ammonium nitrate	-
CV%	Coefficient of variation	%
d	Skewness of Equation 2.3	-
D_c	Critical deficit	mm
DM	Dry matter	g m^{-2} or t ha^{-1}
E	Potential evapotranspiration	mm
Ep	Penman evapotranspiration	mm
Es	Soil Evaporation	mm
FSA	Fraction of senesced leaf area	-
g	Asymptotic value of TLAI (Equation 5.2)	m^2 m^{-2}
GAI	Green area index	m^2 m^{-2}
GLAI	Green leaf area index	m^2 m^{-2}
h	Curvature of Equation 5.2	-

HI	Harvest index	$g\ g^{-1}$
I	Irradiance incident on a leaf (Equation 2.4)	μ mol PPFD $m^{-2}\ s^{-1}$
i	Inflection point of Equation 5.2	days
IRGA	Infra red gas analyser	-
k	Extinction coefficient	-
LA	Area of an individual leaf (Equation 2.3)	cm^2
LAI	Leaf area index	$m^2\ m^{-2}$
LAI_{crit}	Critical LAI	-
LN	Number of fully expanded leaves	-
LTM	Long term mean	-
m	Slope of Equation 5.2 at inflection point (i)	LAI day^{-1}
N	Nitrogen	-
P	Phosphorus	-
p	Theoretical maximum value of RI_{cum} (Equation 5.4)	MJ m^{-2}
P_{2000}	Rate of leaf photosynthesis at 2000 PPFD	μ mol CO_2 $m^{-2}\ s^{-1}$
PAR	Photosynthetically active radiation	MJ m^{-2}
P_g	Gross photosynthetic rate (Equation 2.4)	μ mol CO_2 $m^{-2}\ s^{-1}$
PLA	Leaf area per plant	m^2
P_{max}	Maximum rate of leaf photosynthesis (Equation 2.4)	μ mol CO_2 $m^{-2}\ s^{-1}$
PPFD	Photosynthetic photon flux density	μ mol $m^{-2}\ s^{-1}$
PS	Potassium sulphate	-
PSMD	Potential soil moisture deficit	mm
q	Curvature of Equation 5.4	-
R	Curvature of asymptotic curve (Equation 2.4)	-
r	Midpoint of Equation 5.4	days

RI	Daily solar radiation interception	MJ m^{-2}
RI_{cum}	Accumulated intercepted solar radiation	MJ m^{-2}
RI_{frac}	Daily fractional solar radiation interception	-
RMSD	Residual mean squared deviations	-
RUE	Radiation use efficiency (solar radiation)	g DM MJ^{-1}
s.e.	Standard error of the mean	-
SLA	Specific leaf area	m^2 g^{-1}
SLN	Specific leaf nitrogen	g N m^{-2}
SLP	Specific leaf phosphorus	g P m^{-2}
t	time	days
T_b	Base temperature	°C
TLAI	Total leaf area index	m^2 m^{-2}
T_{mean}	Mean air temperature	°C
T_{opt}	Optimum temperature	°C
TSP	triple super phosphate	-
Tt	Thermal time	°Cd
X_0	Position of largest leaf (Equation 2.3)	(n)
Y_0	Area of largest leaf (Equation 2.3)	cm^2
α	Initial slope of Equation 2.4	μ mol CO_2 μmol^{-1} PPFD
θ	Curvature of Equation 2.4	-
τ	Proportion of ground cover (Equation 3.1)	-
φ	Soil diffusivity constant (Equation 3.3)	mm $day^{-1/2}$

Chapter 1. General introduction

1.1 Environmental factors that determine crop yield

Understanding the processes of crop growth and development is central to the development of economically optimum and environmentally sustainable best management practices for crop production. Isolating the principal mechanisms of growth and development and quantifying their responses to the environment are important steps towards achieving this. This is the science of crop physiology (Hay and Walker, 1989) or the study of the processes within crops and how they interact with the environment.

In the absence of pest and diseases weather is the dominant determinant of crop yield (Monteith, 2000). Furthermore, when temperature, moisture and nutrients are non-limiting, solar radiation is the environmental factor that limits crop yield (Loomis and Williams, 1963). Crop production is the process of solar energy capture by crop leaves and its conversion into useful forms of chemical potential energy by photosynthesis (Hay and Walker, 1989). Crop biomass is the product of accumulated intercepted solar radiation (RI_{cum}; MJ m^{-2}) and the efficiency with which it is used to produce biomass, commonly called the radiation use efficiency (RUE; g DM MJ^{-1}) (Monteith, 1977). However, not all crop biomass is economically valuable, and the harvest index (HI; g g^{-1}) quantifies the proportion of total biomass that is in the economically valuable part of the crop. Crop yield is then the product of these three variables (Equation 1.1) (Gallagher and Biscoe, 1978).

$$Yield = RI_{cum} \times RUE \times HI$$

Equation 1.1

In non-limiting environments RUE (Sinclair and Muchow, 1999) and HI (Hay, 1995) are stable. Incident solar radiation then drives yield by altering RI_{cum} (Equation 1.1). Water and nutrients can be adjusted by applying irrigation and fertiliser respectively. However, temperature is generally beyond the control of field crop growers. Temperature can be regarded as a second factor that determines potential yield. Temperature affects RI_{cum} by determining crop development including leaf appearance rates and hence the proportion of solar radiation intercepted (RI_{frac}). Temperature also alters crop duration, thereby altering the total solar radiation incident on a crop (Muchow *et al.*, 1990). Temperatures outside the optimum range may also limit RUE (Sinclair and Muchow, 1999) through a reduction in photosynthesis or increased respiration rates. For example, in maize crops mean daily air temperatures less than 16 °C reduce RUE (Wilson *et al.*, 1995).

In marginal environments, scarcity of moisture and nutrients will reduce one or more of the variables in Equation 1.1 and actual yield will consequently be less than potential.

1.1.1 Nutrient responses

There are two common methods for quantifying crop responses to nutrient supply. Firstly, yields can be regressed against nutrient supply, usually resulting in an asymptotic curve. Such responses are frequently site and season specific and simply summarise the response with little general applicability beyond the experimental site. Unfortunately, nutrient responses have traditionally been examined using this approach (e.g. Greenwood *et al.*, 1980). Thus, utilising such site and season specific results requires the unrealistic objective of examining response curves for every conceivable site and season combination. An alternative method for examining crop responses examines individual growth processes (Equation 1.1) and their responses to nutrient supply. The results of this approach are more widely applicable as they account for the influence of other environmental factors.

1.2 Linking crop physiology and simulation

Examining individual crop processes is a necessary reductionist part of examining the whole crop and this cannot be done in isolation. A crop is more than the sum of its individual processes but it can be explained in terms of the processes and how the interact (Thornley and Johnson, 2000). The interactions between these processes and the environment can be examined using crop simulation models.

Models are generally described as either mechanistic or empirical. An empirical model is a description of a given data set and does not imply any understanding of the biological mechanisms underpinning a response. An example of an empirical model is a classical fertiliser response curve. A mechanistic model describes the processes involved in a response to a certain environmental stimulus based on an underlying knowledge of the physiology involved (Thornley and Johnson, 2000).

By definition, models are abstractions and therefore do not include every level of detail. As scientific tools, simulation models should avoid erroneous complexity that will hinder their interpretation (Sinclair and Seligman, 1996). For example, crop yield is the product of photosynthesis; however, simulating the reaction rates of individual Calvin cycle enzymes is unlikely to enhance the understanding of crop yield. Therefore, models generally include processes at only 1 or 2 levels of complexity below the variable being simulated.

Mechanistic models use a set of equations that conceptualise crop growth (Ritchie, 1991) as developed from sound field experiments. Continued progress in crop physiology will involve both field physiology experiments, crop simulation models and their collaborative efforts (Hay and Walker, 1989).

Crop simulation models have many uses both as predictive tools and in the development of new ideas (Boote *et al.*, 1996; Hammer *et al.*, 2002). From a scientific perspective they are most useful as a set of quantitative hypotheses that are testable by subsequent experimentation (Boote *et al.*, 1996). The model is then a unique method of communicating ideas between scientists. An example of this is the simulation analysis of Jamieson and Semenov (2000), which showed that N affected wheat yield by altering green leaf area index (GLAI) and maintaining a stable radiation use efficiency (RUE). For this application, accuracy of simulated yields is not the only attribute on which a model should be judged. The framework also needs to be based on sound physiological principals that can be used to test relevant hypotheses (Jamieson *et al.*, 1998b).

1.3 Physiology of nitrogen and phosphorus responses

The link between crop physiology and simulation modelling is well demonstrated by a set of analyses of maize responses to N supply. Muchow (1988a) demonstrated that leaf area was reduced in N deficient maize to maintain specific leaf nitrogen (SLN; leaf N concentration on an areal basis) above 0.55 g N m^{-2}. Muchow and Davis (1988) then established that RUE was reduced by N deficiency and that it was closely related to the SLN. Muchow and Sinclair (1994) showed that these RUE responses would be expected based on leaf photosynthetic rates. Muchow (1988b) showed that lack of nitrogen had a minor effect on HI, and that this was related to the remobilisation of N to the developing grain. Thus to varying extents all of the variables in Equation 1.1 were sensitive to N supply. These responses were used to create a simulation model of N effects on maize yield (Muchow and Sinclair, 1995; Sinclair and Muchow, 1995). A sensitivity analysis indicated that the minimum grain N concentration had a major effect on simulated yield. Grain yield could be increased in low N environments by selecting varieties with a low minimum grain N content. Thus, studying the individual

processes of the N response resulted in a potential method for improving yield in these N limited environments.

The response to N of many crops, including maize, has been extensively researched. However, phosphorus (P) supply limits yield on much of the world's arable land (Vance *et al.*, 2003) and economic P reserves may be depleted by 2050-2070 (Anonymous, 1988). Therefore examining P responses is of importance in sustaining high crop yields. Also, including P as a constraint will be important in using simulation models to address sustainability issues (Probert and Keating, 2000). Yield responses to P have been reported for both maize and sweet corn (e.g. Bole and Freyman, 1975). The processes of P uptake from the soil are well understood (Barber, 1995) and some recent simulation models have included P uptake (Daroub *et al.*, 2003; Jones *et al.*, 1984; Probert, 2004). In contrast, the crop growth processes affected by P supply have received less research.

Notable exceptions are the studies of Plenet *et al.*, (2000a; 2000b) which showed P affected RI_{cum}, but that RUE and HI were stable in maize. However, in this study soil P was comparatively high (Olsen P > 23 $\mu g\ ml^{-1}$) and yield responses to P were moderate (~14%) compared with the literature (e.g. 35-60% Obreza and Rhoads, 1988). Mean air temperatures during the experiments of Plenet *et al.* (2000a; 2000b) were near optimum for maize (~ 23-24 °C), but *Zea mays* is sometimes grown in considerably cooler climates. For example in Canterbury, New Zealand, mean air temperatures are ~15 °C during the November to April growing season. Some evidence also suggests that sweet corn is more responsive to P than maize (Bole and Freyman, 1975). Therefore, in the present study the responses of sweet corn crop growth and development processes (Equation 1.1) to P supply in a cool temperate climate with a low soil P were examined.

1.4 Aims and objectives

The principal aim of the research presented in this thesis was to determine the key crop physiological variables that respond to a limited P supply in 'Challenger' sweet corn crops in the cool temperate climate of Canterbury. It is expected that the mechanisms identified would be appropriate for incorporation into universal crop models of crop growth and development of sweet corn.

There were three main objectives; and each related to one of the variables in Equation 1.1. These were to examine the response to P supply of:

- crop biomass and partitioning (HI)
- RI_{cum}
- RUE

A fourth objective was to:

- integrate these responses into a simple simulation model and examine the implications of a limited P supply across multiple sites and seasons using long-term weather records.

1.4.1 Thesis structure

The general structure and the focus of each of the eight chapters are outlined in Figure 1.1.

Chapter 2 reviews relevant literature for both sweet corn and maize. Initially each mechanism is examined in non-limiting situations. Where literature is available the effects of P and N limitations are then outlined. Chapter 3 outlines the details of five experiments and the measurements taken from each. These experiments form the basis of the results in Chapters 4-6.

Chapter 4 is an agronomic results chapter that describes total crop yield, biomass partitioning and quality responses of 'Challenger' sweet corn to both P and N. This chapter also examines phenological development in response to P. Analysis in Chapter 5 focuses on RI_{cum} and its component processes for 'Challenger' sweet corn in response to P. In Chapter 6 sweet corn RUE and leaf photosynthesis are examined while in Chapter 7 the results of Chapters 4, 5, and 6 are combined into a simple model of sweet corn growth and development where P is limiting. Chapter 8 provides a general discussion of the implications of the results from the previous chapters and addresses the aims and objectives outlined in Section 1.4. Chapter 8 also discusses the potential for further research.

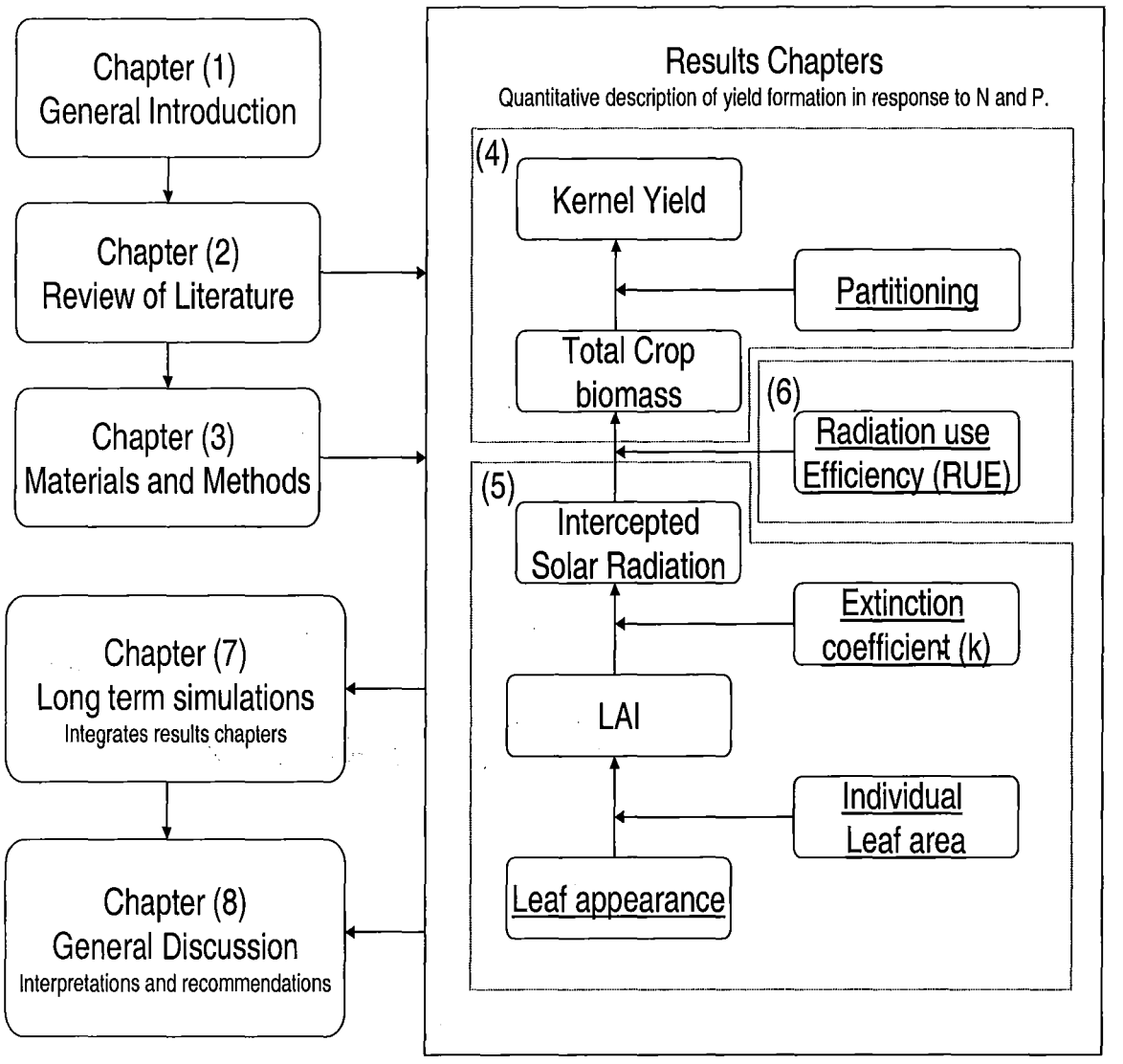

Figure 1.1 Outline of thesis structure. Each arrow represents a link between the chapters and processes. In the results chapters the underlined processes are the crop level responses which produce the other processes. The representation of the processes in results chapters is adapted from Westgate *et al.* (2004).

Chapter 2. Review of the literature

2.1 Introduction

The literature regarding the agronomic management of grain maize is extensive compared with that for sweet corn, reflecting the relative global importance of the two crops. In recognition of their similarities, this review is based on literature from either crop. However, there are key management differences between the two crops, so wherever possible research specifically targeted for sweet corn is highlighted.

In this chapter previous results from both empirical and more mechanistic studies are examined in three parts. The first part examines agronomic responses of sweet corn yield to N and P supply. In the second, the important variables of maize and sweet corn crop growth and development in response to the environment and N and P limitations are described. The final part examines how these variables can be used to create a simple semi-mechanistic framework for examining maize yields and then discusses the implications of using this framework to examine sweet corn N and P responses.

The experiments in this thesis were located in a cool temperate climate at Lincoln, Canterbury, New Zealand (Chapter 3). This location is characterised by cool temperatures (mean monthly minimum air temperatures 8.0 - 11.5 °C and mean monthly maximum air temperatures 17.5 – 22.5 °C) during the maize/sweet corn growing season (November-April). Therefore the effect of this cool temperature range on the processes examined is highlighted.

2.2 Agronomic fertiliser response

Successive increments in nutrient supply that give an asymptotic yield response are the common form described in the literature (Sections 2.2.1 and 2.2.2). This general nutrient response is expected because for each increment the nutrient is acting against a smaller

deficiency. However, the magnitude of response is dependent on the base soil nutrient levels, and the environmental and management factors that determine the maximum yield (asymptote). Two examples of these asymptotic curves in sweet corn follow.

2.2.1 Nitrogen

Bole and Freyman (1975) grew sweet corn at two sites (Cranford in 1971 and 1972; and Taber in 1972) in Canada in two seasons. An asymptotic increase in kernel yield to N fertiliser rates of 0-200 kg N ha^{-1} was found at all three site-season combinations, but the shape and magnitude of responses differed. The potential yield was greater (~10 t ha^{-1}) in 1971 than in 1972 (~6-7 t ha^{-1}) (Figure 2.1a) probably due to environmental differences between the two seasons.

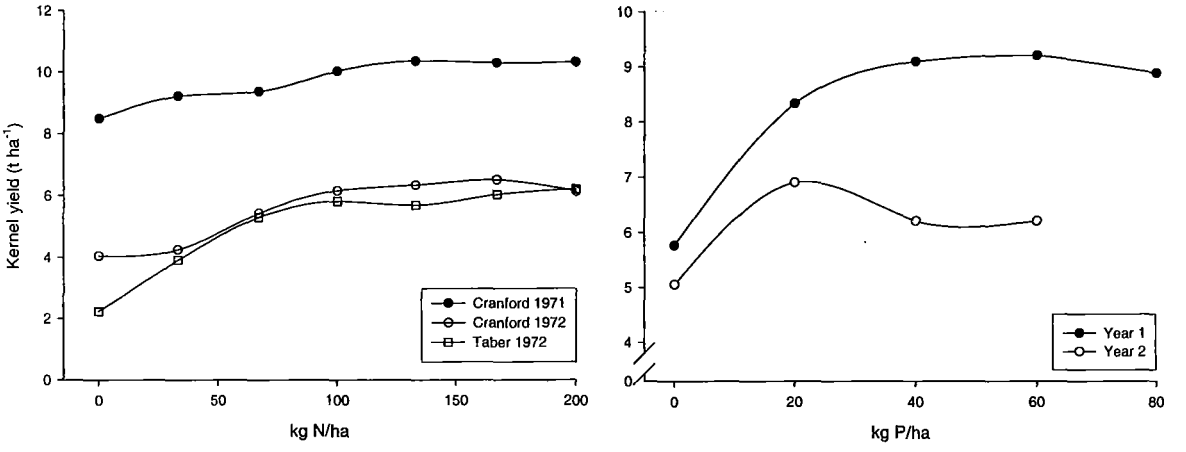

Figure 2.1 Kernel yield response of sweet corn to: applied fertiliser nitrogen at two sites in Southern Alberta Canada in 1971 and 1972 (a); and applied P fertiliser in Florida, USA in two years (actual years not provided by the authors) (b). (After Bole and Freyman, 1975; Sanchez *et al.*, 1989).

2.2.2 Phosphorus

Similarly, Sanchez *et al.* (1989) demonstrated an asymptotic increase in sweet corn kernel yield with P fertiliser rates ranging from 0-80 kg P ha^{-1}, at a single site in two years. Again the responses were markedly different between seasons with maximum yields of ~9.2 t ha^{-1} with ~60 kg P ha^{-1} in year 1 but only 6.1 t ha^{-1} with 20 kg P ha^{-1} in year 2 (Figure 2.1b). The lower potential yield in the second season was due to water stress caused by low rainfall. This example highlights the over-riding importance of the environment in determining the shape of these nutrient responses. A lower asymptote in the second season meant that potential yield was obtained with less fertiliser P than in the first season.

A plethora of literature shows similar responses of sweet corn to both N (e.g. Salardini *et al.*, 1992) and P (e.g. Prasad *et al.*, 1988; Sanchez *et al.*, 1991; Zaharah and Sharifuddin, 1995). In each case results have been statistically analysed with either response curves or analysis of variance, which simply indicate the probability of obtaining the same response in an identical environment. A further example in the literature showed no yield response of sweet corn to P fertiliser (Kabir and Koide, 2002) which highlights the site and season specificity of the previous examples.

Such responses have been collated to give recommended soil nutrient levels. For example, in New Zealand the recommended Olsen P level on a low P retention site (<30%) for sweet corn is 30-35 μg ml^{-1} (Clarke *et al.*, 1986), compared with 15 μg ml^{-1} for maize (White *et al.*, 1999). The implication is that sweet corn requires higher soil P levels for maximum yields than maize. This is consistent with results from Bole and Freyman (1975), who compared the

two crops at three sites and found increases of 7-12% for maize grain yield, but 10-17% for sweet corn yield across P fertiliser rates from 0-60 kg P ha^{-1}.

2.3 The effect of environment and nutrients on maize and sweet corn growth

Following extensive agronomic experiments an alternative approach using a semi-mechanistic crop model has been developed (Reid, 2002) and tested in maize (Reid *et al.*, 2002). Temperature, solar radiation, and moisture are used to simulate potential yield (Wilson *et al.*, 1995). This potential yield is then penalised using a relative yield that is related to a scaled index of nutrient supply. It seems likely that this approach would work well in examining sweet corn N and P responses. This approach reduces the site and season specificity (through its effect on simulated potential yield). However, the mechanisms of yield loss under N and P deficiencies are not examined. A focus of the present study is to examine the mechanisms by which yield potential is reduced when N and P supply are limiting. To do this the influence of nutrient supply on growth and development of sweet corn and maize crops is reviewed. This review initially examines the value of each variable in a non-stressed environment. The effects of nutrient stresses, particularly N and P, are then examined. In some cases other environmental stresses (e.g. moisture limitations) have a similar effect to these nutrients and therefore these responses have been included.

Two components of crop production require attention in crop physiological analyses. Firstly 'growth' is defined as simply an increase in mass of a plant or crop. Secondly 'development' is considered the irreversible progression through fixed and species-specific stages of a crops life cycle (Goudriaan and van Laar, 1994). These two processes are linked, but for simplicity they are usually treated separately. For example, leaf appearance is a development process, because each leaf represents a separate stage, but it is also important for the interception of

solar radiation - a determinant of potential growth. This review examines the two separately. Firstly growth as it pertains to kernel yield is reviewed and then reproductive development is examined. Kernel yield is described by Equation 1.1 and each of the variables along with their component processes are discussed in turn.

2.3.1 Radiation interception, green leaf area index (GLAI) and extinction coefficient (k)

Radiation interception is determined firstly by the availability of incident solar radiation. However, with the exception of location and sowing date (Rogers *et al.*, 2000; Sorensen *et al.*, 2000; Stone *et al.*, 1998b) crop management does not influence the amount of incident radiation and therefore it will be disregarded in this review.

Radiation interception is also determined by the area of crop leaves present at any point in time. This can be quantified by the leaf area index (LAI), or the area of leaves covering a given area of soil. Only the photosynthesising green leaves are important for crop growth so this is quantified as green LAI (GLAI) or the total LAI minus the senesced leaves. The fraction of solar radiation intercepted at any given time is related to GLAI by an exponential function (Equation 2.1) (Thornley and Johnson, 2000).

$$RI_{frac} = 1 - e^{-k \times GLAI}$$

Equation 2.1

Where RI_{frac} is the daily fraction of solar radiation intercepted, and k is the extinction coefficient.

The extinction coefficient is a measure of how effective a given GLAI is at intercepting solar radiation. Differences in k are principally associated with changes in leaf angle (Hay and Walker, 1989). Flat leaved crops have a higher k and a lower critical LAI (LAI for RI_{frac} = 0.95), compared with erect leaved crops (Monteith, 1969). A crop canopy is said to be closed when LAI_{crit} has been obtained. After this changes in GLAI have only minor effects on RI_{frac} (Jamieson *et al.*, 1998a). In sweet corn crops in Canterbury GLAI is generally low (<4) for much or all of the season (e.g Stone *et al.*, 2001b) and hence changes in GLAI have major implications for radiation interception. In contrast, crops such as wheat may quickly reach LAI_{crit} (e.g. Jamieson and Semenov, 2000) and therefore further changes in GLAI have only minor implications for RI_{frac}.

The extinction coefficient is greater in the early morning and late afternoon compared with solar noon. At these times solar radiation is incident at a greater angle and therefore has to pass through relatively more leaf area. However, a weighted mean average over a day can successfully integrate these diurnal changes in k (Flenet *et al.*, 1996; Maddonni *et al.*, 2001b). Therefore, this effect is generally ignored in the use of simulation models and a single k value assigned.

A wide range (0.37-0.69) of k values has been reported for maize (Table 2.1). At low latitudes (15°) k will be lower than at higher latitudes (45°). This is because solar zenith angles at midday will be greater at higher latitudes and hence the direct beam solar radiation will pass through relatively more leaf area. This can be demonstrated by plotting experimentally determined k against latitude (Figure 2.2). Therefore k will be specific to the experimental location and using an assumed extinction coefficient, may lead to errors in calculating RI_{frac}. For example Stone *et al.* (2001a) used k = 0.4 based on the data of Muchow and Davis (1988)

(14° 28' S), but the crop was grown at 43° 38' S. Preferably k should be determined for each experiment.

Table 2.1 Range of reported daily k values for maize crops.

k	*Treatments*	*Reference*
0.35-0.48	Plant spacing and population	*(Westgate *et al.*, 1997)
0.31-0.74	Crop development stages	(Lizaso *et al.*, 2003)
0.65	Review	(Monteith, 1969)
0.58	Method of measurement	*(Peressotti *et al.*, 1999) (●)
0.46	Five hybrids	(Birch *et al.*, 1999) (♦)
0.46-0.62	Three hybrids	*(Maddonni and Otegui, 1996) (■)
0.34-0.47	Row spacing	(Flenet *et al.*, 1996) (▲)
0.37-0.65	Row spacing / plant population	*(Maddonni *et al.*, 2001c)
0.4	Model	(Muchow *et al.*, 1990) (○)
0.47	Two years	*(Kiniry *et al.*, 2004) (□)
0.52	Planting densities	*(Gallo *et al.*, 1993)
Range	0.37-0.69	

* Point measurements taken at midday only.

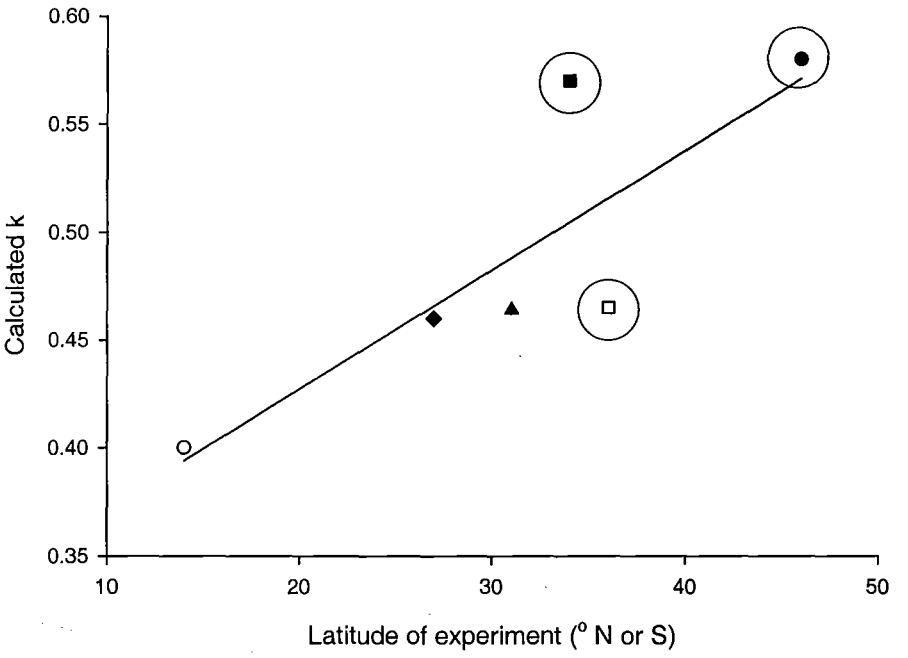

Figure 2.2 Calculated k values of maize against latitude for selected references given in Table 2.2. Due to the importance of both row spacing and plant population in determining k, only data with a row spacing of 0.5-0.76 m and a plant population 5.9-8.4 plants m^{-2} have been used. Note: The circled values were calculated from spot readings taken at approximately midday and may therefore be misleading.

If k is constant for a given set of conditions (i.e. crop, plant population, and location), then changes in RI_{frac} due to environmental stress are directly associated with GLAI. Changes in RI_{cum} result from changes in both maximum GLAI and the temporal pattern of GLAI and are reduced under conditions of limited N (Muchow, 1994) or P (Plenet *et al.*, 2000b).

In non-limited conditions the temporal pattern of GLAI in maize and sweet corn is dependent on the leaf appearance rate and follows a consistent pattern to reach a maximum at silking (Figure 2.3). At silking all of the leaves have appeared and the maximum GLAI therefore

depends solely on the summed areas of the individual green leaves. After silking major leaf senescence decreases GLAI (Figure 2.3).

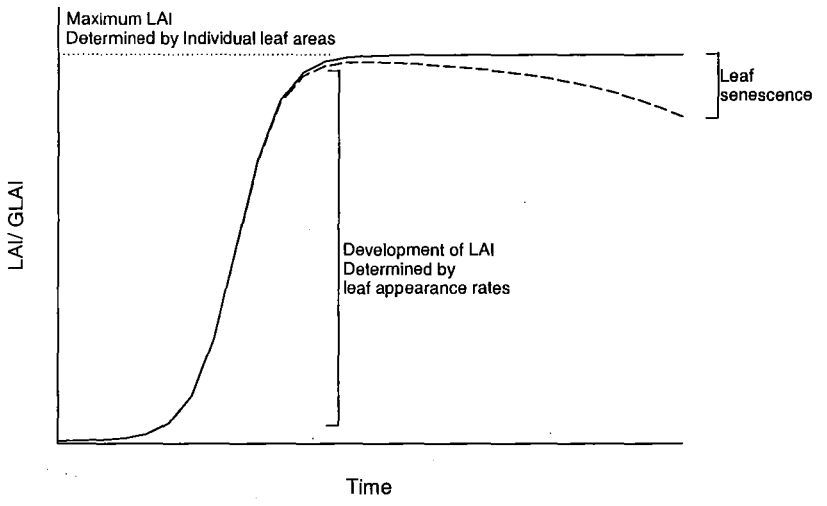

Figure 2.3 Representation of LAI (solid line) and GLAI (dashed line) through time for maize and sweet corn crops.

It follows that the instantaneous GLAI is the product of three variables (Equation 2.2).

$$GLAI = (PLA - (PLA \times FSA)) \times \text{plant population}$$

Equation 2.2

Where PLA = leaf area per plant (m^2), FSA is the fraction of senesced leaf area, and plant population is given in plants m^{-2}.

Plant population is a factor determined by sowing rate and will not be considered further, except for its effect on individual growth processes. PLA expansion parallels GLAI whereby the temporal pattern is determined by the rate of appearance and area of individual leaves

prior to silking. Maximum PLA at silking is the sum of all individual leaf areas. Prior to silking PLA is the sum of all fully expanded leaves plus the summed areas of leaves that are expanding but have not yet fully expanded. PLA is reduced post-silking as leaf senescence occurs and FSA increases. The influence of nutrients on RI_{cum} can therefore be examined by determining their impact on each of the components of GLAI (i.e. rate of leaf appearance, the area of individual leaves, and FSA).

2.3.1.1 Leaf appearance

The appearance of leaves determines the rate at which the maize or sweet corn crop obtains maximum GLAI. The appearance of leaves can be divided into two parts; the appearance of visible leaf tips, and the appearance of fully expanded leaves (leaf collar visible).

Sweet corn and maize leaf tips become visible in a linear fashion in relation to thermal time (Tt) accumulation (T_b=8°C) (Section 2.5.1, Equation 2.5). The reciprocal of a regression between Tt and the number of visible leaf tips gives the phyllochron (°Cd leaf tip^{-1}). Typical maize phyllochrons are 35-50 °Cd leaf tip^{-1} (Birch *et al.*, 1998c; Birch *et al.*, 1998d) in unstressed conditions. Rogers *et al.* (1999) concluded that sweet corn phyllochrons were shorter (i.e. 25°Cd based on Stone *et al.*, 2001b) than maize (36°Cd). However, their conclusion was based on a limited data set and requires further examination.

The literature shows that abiotic stresses can reduce leaf appearance rates. Specifically, limited N (Muchow, 1988a), P (Colomb *et al.*, 2000; Plenet *et al.*, 2000b) and lime (Sierra *et al.*, 2003) have all been shown to delay the appearance of visible leaf tips in maize. For example Plenet *et al.* (2000b) found that for leaves 4 to 9 maize plants receiving no P fertiliser had a phyllochron of 65 °Cd leaf tip^{-1}, whereas plants receiving 53 kg P ha^{-1} had a phyllochron of 47°Cd leaf tip^{-1}.

Delays in maize leaf tip appearance may result from an increased plastochron (°Cd between successive primorida) as reported for wheat (Rodriguez *et al.*, 1998a). Alternatively a decreased assimilate supply may delay primordia extension and hence the phyllochron would appear to be longer. This hypothesis is supported by results from Birch *et al.* (1998d) where shading treatments increased the phyllochron in field grown maize from 35 to 60 °Cd. These results are in accord with the growth chamber results of Bos *et al.* (2000b), where maize was grown with either 104, 185 or 277 μmol PPFD m^{-2} s^{-1} at four fluctuating temperatures (12h/12h of 13/8, 18/3, 23/18 and 28/23 °C). A reanalysis of these data, using a linear regression of leaf appearance rate (leaves day^{-1}) against mean temperature (°C) and an assumed T_b of 8°C, gives phyllochrons of 46.7 °Cd leaf tip^{-1} in the 104 PPFD treatment and 39.5 °Cd leaf tip^{-1} in the 277 PPFD treatment. Similarly using a range of sowing dates in a glasshouse Gmelig Meyling (1973) showed that increasing light intensities gave an increased leaf appearance rate in maize. However, in this experiment light intensity was confounded with temperature as it was not measured for each crop. But for both Birch *et al.* (1998d) and Bos *et al.* (2000b) air temperature was monitored for each crop and hence the differences in leaf appearance were not due to changes in temperature. However, the light treatments in these experiments may also modify the apex temperature of the plants. This may have confounded the results, and therefore caution must be applied to their interpretation.

In the experiment of Gmelig Meyling (1973) there was a strong relationship between relative growth rate (g g^{-1} day^{-1}) and leaf appearance rate. Bos *et al.* (2000a) showed a strong relationship between plant growth rate (g $°Cd^{-1}$) and maize leaf appearance rate across a range of plant densities (between 1/∞ and 1230 000 plants ha^{-1}) in field grown maize. However, in

these studies it is unclear whether the leaf appearance rate or the plant growth rate was the causal factor.

All these data support the hypothesis of McMaster *et al.* (2003) that in spring wheat, and probably other crops, "factors other than temperature exert a major influence on the cell expansion component of the phyllochron, explaining why the plastochron, or leaf primordia initiation, is more strongly related to temperature than is the phyllochron".

In contrast to leaf tips the appearance of fully expanded leaves in maize is exponential with Tt (Muchow and Carberry, 1989). This curve is initially approximately linear, but as the stem elongates, and the staminate apex of the plant emerges from the soil, the upper leaves are 'pushed out' at a faster rate. Rapid stem elongation begins when 7 leaves have fully expanded (Robertson, 1994), irrespective of the final number of leaves on a hybrid and water status.

As for leaf tip appearance, fully expanded leaf appearance is more rapid in sweet corn than maize (Rogers *et al.*, 1999). There is little data regarding N and P limitations on fully expanded leaf appearance. However, severe nutrient limitations that limit leaf tip appearance, will probably also limit the appearance of fully expanded leaves.

2.3.1.2 Area of individual leaves

The area of individual maize and sweet corn leaves is related to their main stem position. The first leaf to appear is comparatively small with each subsequent leaf having a progressively larger area up to a maximum which is then followed by a decline in leaf area for each successive leaf. This produces a bell-shaped curve (Dwyer and Stewart, 1986a) (Equation 2.3) between individual leaf area and leaf position which has been used with both maize and sweet corn (e.g. Elings, 2000; Muchow and Carberry, 1989; Rogers *et al.*, 1999).

$$LA = Y_0 \times e[c(X - X_0)^2 + d(X - X_0)^3]$$

Equation 2.3

Where LA is the area of a given leaf (cm^2), Y_0 is the area of the largest leaf (cm^2), X is the position of the leaf being estimated, X_0 is the position of the largest leaf, **c** is a dimensionless parameter defining the breadth of the peak, and d is a second dimensionless parameter that defines the skewness of the curve. Increasing values of c make the peak broader, whereas negative values of d skew the peak towards the left.

It is generally only the coefficients for the area (Y_0) and position (X_0) of the largest leaf that differ markedly. Both are closely related to the final number of main stem leaves per plant (Birch, 2003; Keating and Wafula, 1992) in non-stressed conditions. Late maturing hybrids (i.e. having a greater final main stem leaf number) have a greater value of both X_0 and Y_0. X_0 is consistently two thirds of the final number of leaves (Birch *et al.*, 1998b).

The consistency and shape of the bell-shaped curve can be accounted for by the effect of both the duration of leaf expansion and the expansion rate of each individual leaf. Normalised curves of individual leaf area, expansion duration and expansion rate follow broadly the same pattern of the bell-shaped curve (Stewart and Dwyer, 1994). That is, X_0 is the largest leaf because it has both the longest duration of leaf expansion and the most rapid rate of expansion.

However, when stresses are applied to the crop it is principally only Y_0 that varies, with X_0 remaining relatively constant. In 'Challenger' sweet corn under varying degrees of moisture stress (PSMD 90-403 mm), X_0 was unchanged but Y_0 decreased (Stone *et al.*, 2001b).

Although this bell shaped curve was not explicitly fitted the data of maize leaf area in response to both P (Colomb *et al.*, 2000; Plenet *et al.*, 2000b) and liming treatments (Sierra *et al.*, 2003) indicate that X_0 was unchanged whereas Y_0 was reduced in treatments where the crops were stressed.

In a growth chamber experiment, Assuero *et al.* (2004) showed that the reduced area of individual leaves in P deficient maize was associated with a reduction in cell number per leaf and not a reduction in cell size. There were fewer cells per leaf due to a decrease in the size of the leaf zone where cells were produced and a decreased production rate within that zone. This reduction in cell production may have been caused by a lack of P as a constituent of bio molecules or some type of hormonal control of cell division (Assuero *et al.*, 2004). Alternatively there may have been a carbohydrate limitation on cell division. This would be consistent with the results of Granier and Tardieu (1999) which showed that in sunflower the radiation intercepted by the plant during the initial period of cell division was pivotal in determining the subsequent area of an individual leaf.

It has been shown that maize adjusts leaf size to maintain specific leaf N (SLN, g N m^{-2} leaf) above a value of 0.55 (Muchow, 1988a). This value most likely represents the minimum photosynthetic rate required to produce the maintenance respiration requirements of an individual leaf. The similarities between sweet corn and maize suggest that a similar pattern may occur in sweet corn. It is unknown whether a similar mechanism is used to maintain leaf P levels above a minimum concentration per unit of leaf area.

2.3.1.3 Leaf senescence

Leaf senescence in maize is commonly quantified using the fraction of senesced area (FSA). Maize FSA increases exponentially with Tt (°Cd) (Muchow and Carberry, 1989). This

exponential increase is due to the remobilisation of carbon and N from older leaves to developing reproductive structures. As grain growth increases rapidly the demand for N is increased and hence leaf senescence increases because soil N uptake can no longer fulfil crop requirements. In grain maize 27-40% of N in mature grains may be remobilised from leaves (Ta and Weiland, 1992). Imbalances in the source: sink ratio during maize grain filling can also lead to acceleration of leaf senescence (Rajcan and Tollenaar, 1999). Borras *et al.* (2003) showed that a two-stage process could describe FSA. In the 1st stage FSA was minimal and major senescence (stage II) began approximately 400-450 °Cd after sowing regardless of the growing environment.

FSA is normally of a lesser magnitude in sweet corn than in maize crops. This is because sweet corn is harvested at an immature stage before significant amounts of N have been remobilised. For example, in unstressed treatments, FSA did not exceed 0.2 in 'Challenger' sweet corn (Stone *et al.*, 2001b) but was 1.0 at maturity for maize (Stone *et al.*, 1999). The data of Rogers *et al.* (1999) showed that at a similar plant development stage FSA was less in sweet corn than in maize. This implies that sweet corn was more effective at maintaining a green canopy than maize and suggests this is an aspect of sweet corn crop growth where specific studies may be necessary.

Senescence is primarily associated with the internal remobilisation of nutrients. Nutrient deficiencies accelerate senescence and hence reduce GLAI as shown for N in grain maize (Muchow, 1988a, 1994).

The limited maize data set in response to P supply is inconclusive. From a controlled environment study in young maize (0-30 days after planting) it was concluded that P

remobilisation regulated leaf senescence (Usuda, 1995). However, these results may not apply to a field situation. In field grown maize P limitation had a minor effect in both accelerating (Plenet *et al.*, 2000b) and delaying (Colomb *et al.*, 2000) leaf senescence. In a field situation leaf senescence in maize is probably limited more by the environment than by P supply. Given the differences in senescence between maize and sweet corn and the different P responses, determining the specific effect of P supply on sweet corn senescence is necessary.

2.3.1.4 Reconstruction of GLAI

For a given crop the components of GLAI (leaf appearance, individual leaf area, and FSA) can be used to reconstruct GLAI. This may be necessary in two situations. Firstly for construction of a crop model (Section 2.6) it is necessary to calculate GLAI so that RI can be calculated. Secondly in an experiment it may be necessary to calculate GLAI to compare RI and RUE in response to given treatments (e.g. Stone *et al.*, 2001a).

There are a number of instruments that can be used to directly measure either GLAI or RI. A ceptometer can be used to measure solar radiation above and below a canopy and hence RI can be calculated as the difference between the two. However, this method is specific to the time of day of each measurement. At low LAI, RI_{frac} differs between midday and early morning. A more robust method is to use tube solarimeters to log data at hourly intervals (e.g. Muchow and Davis, 1988). This method successively integrates diurnal changes in RI_{frac}. However, these instruments are costly which limits their widespread use across a number of treatments and replicated plots within an experiment. Furthermore, tube solarimeters and ceptometers do not quantify GLAI and, unless assumptions are made about k, they simply give values for RI_{frac}.

GLAI can also be obtained from destructive samples. However, edge effects and the frequency of measurements means that plot sizes become unmanageably large to achieve this for a full growing season. Therefore non-destructive methods such as the LAI-2000 canopy analyser are used. This method indicates the temporal distribution of GLAI; however, the relationship between destructive measurements of GLAI and measured GLAI is not always 1:1 (Wilhelm *et al.*, 2000).

In a crop such as sweet corn where GLAI is less than critical LAI (e.g. > 3 Stone *et al.*, 2001b) for most if not all of the season, accurate determination of GLAI is required at frequent intervals. In this case reconstruction of the canopy GLAI is appropriate. Stone *et al.* (2001b) showed a close agreement between reconstructed canopy GLAI and destructive harvests of GLAI between 0-3.

Their method was to reconstruct leaf area per plant (PLA) and multiply this by the plant population on any given day. To achieve this, the number of fully expanded leaves was predicted from an exponential relationship with Tt (Section 2.3.1.1), the individual areas of these fully expanded leaves (Section 2.3.1.2) were then summed to give fully expanded leaf area per plant. To account for leaves that had appeared (leaf tips), but had not fully expanded it was assumed that there was a linear increase in leaf area between leaf tip appearance, predicted from Tt (Section 2.3.1.1), until the appearance of the leaf collar (Section 2.3.1.1). These areas were then summed to give expanding leaf area per plant. The PLA for any day was the sum of fully expanded and expanding leaves. The green leaf area per plant was calculated by subtracting FSA, which was obtained from an exponential relationship with Tt (Section 2.3.1.3). Daily green leaf area per plant was multiplied by plant population to give GLAI.

2.3.2 RUE

RUE is the second variable in Equation 1.1, and represents the efficiency of canopy photosynthesis in using solar radiation to convert CO_2 into DM. RUE can be expressed on the basis of either absorbed or intercepted radiation, on either total solar radiation or photosynthetically active radiation (PAR) (wavelength 400-700 nm), and on above-ground biomass or total crop biomass. In this thesis RUE is reported on the basis of above ground biomass and total solar radiation intercepted by green leaves (senesced leaves ignored). In this review where RUE values have been reported on a PAR basis these have been converted to total solar radiation by assuming that PAR is 50% of solar radiation (Sinclair and Muchow, 1999), unless the conversion factors used have been specifically stated in each experiment.

The literature is replete with examples of RUE in unstressed maize. Some of these have been tabulated (Table 2.2). Extensive reviews by both Sinclair and Muchow (1999) and Kiniry *et al.* (1989) showed that maximum RUE (without environmental stress) in maize is 1.6-1.75 g DM MJ^{-1}. Higher values of RUE have been reported in maize (1.79 g DM MJ^{-1}) by Kiniry *et al.* (2004), however in this experiment the interception of radiation was based on spot measurements at midday which may have underestimated total radiation interception and hence overestimated RUE. The limited values presented for New Zealand (1.2-1.4 Stone *et al.*, 1998c; Stone *et al.*, 1999) were less than those found elsewhere (Table 2.2), probably due to a temperature limitation (Wilson *et al.*, 1995).

Table 2.2 Selected references reporting the range of RUE values for maize.

Maximum value of RUE (g DM MJ $^{-1}$) total Solar radiation	*Reference*
1.55	(Birch *et al.*, 1999)
1.7	(Muchow and Sinclair, 1994)
1.5-1.7	(Muchow, 1994)
1.6	(Muchow and Davis, 1988)
1.6	(Andrade *et al.*, 1993)
New Zealand	
1.4	(Stone *et al.*, 1999)
1.2	(Stone *et al.*, 1998c)

Comparatively few experiments have calculated sweet corn RUE. However, sweet corn and maize are the same species and it is unlikely that RUE differs between the two. One example was Stone *et al.* (2001a) where sweet corn RUE was ~1.75 g DM MJ^{-1} in a fully irrigated crop in Canterbury. This was similar to maximum RUE reported in maize, but is much greater than those reported for maize in New Zealand (Table 2.2). Mean temperature was ~15°C throughout crop growth and, using the temperature function proposed by Wilson *et al.* (1995) (Section 2.3.2.1), the theoretical RUE would have been approximately 1.4 g DM MJ^{-1}. However, the analysis of Stone *et al.* (2001a) assumed k was 0.4 (Muchow *et al.*, 1990) and consequently caution must be applied when interpreting these results (Section 2.3.1). This is particularly important in a crop such as this where the GLAI was low (i.e. <3 Stone *et al.*, 2001b) and errors in k can be expected to markedly affect calculated RI. Further research is required to establish the RUE in sweet corn.

2.3.2.1 Environmental effects

A wide range of environmental factors reduce RUE below its maximum. Any factor that reduces leaf photosynthetic capacity below it normal value can lead to distinct decreases crop RUE (Sinclair and Muchow, 1999). However, both a range of experimental data (Kiniry *et al.*, 1989; Sinclair and Muchow, 1999) and theoretical analysis have shown that increases in maximum leaf photosynthetic rate above normal canopy values result in only minor or negligible increases in RUE (Sinclair and Horie, 1989). Thus there is an upper limit to RUE for a given crop species. In maize this is approximately 1.7 g MJ^{-1} (Table 2.2). The comparative effects of environmental stress on RUE and RI depend both on the factor and the crop under consideration.

Sub-optimal temperatures limit RUE in maize (a C4 species) more than for C3 crops. Using an extensive data set (across years, and sowing dates) Andrade *et al.* (1993) concluded that RUE was maximum at temperatures $\geq$ 20°C and decreased by 0.14 g DM MJ^{-1} for every 1°C decrease in mean temperature. Using a simulation model, Wilson *et al.* (1995) presented a sensitivity analysis showing that maize RUE was maximum (1.6 g DM MJ^{-1}) at a mean daily air temperature $\geq$ 16 °C, and declined linearly to 0 g DM MJ^{-1} at temperatures $\leq$ 8 °C. The data of Muchow and Sinclair (1994) indicated that temperatures between 20 and 32°C had no effect on maize RUE. These data all indicate that temperatures less than ~20 °C limit maize RUE. In most tropical and sub-tropical sites this temperature response is of little consequence, but in temperate areas, such as Canterbury, temperatures < 20 °C are common with mean monthly temperatures between 12-17°C in the October to April growing season.

Drought stress also decreases RUE (Sinclair and Muchow, 1999). Water stress may lead to stomatal closure, decreasing photosynthetic rate and hence RUE. Maize RUE is reduced by water stress and reductions in crop biomass with water stress are associated more with reduced RUE than reduced RI (Earl and Davis, 2003; Muchow, 1989). Stone *et al.* (2001a) showed that sweet corn RUE decreased by 0.2 g DM MJ^{-1} for every 100 mm increase in PSMD. Reductions in total crop biomass were associated with both decreases in RI and RUE, with the relative importance depending on the timing of drought stress.

RUE may differ in crops at different development stages. The general pattern is that RUE is slightly lower during crop establishment, maximal during vegetative stages, and decreases again during reproductive growth. Meaned across four maize hybrids Birch *et al.* (1999) showed that RUE was 1.65 g DM MJ^{-1} before silking and 1.5 g DM MJ^{-1} after silking. This post-silking decrease was attributed to the remobilisation of N from the leaves leading to a decreased leaf photosynthetic rate (Sinclair and Muchow, 1999). Although important for maize this effect is unlikely to occur in sweet corn, where the crop is harvested at a physiologically immature stage before significant N remobilisation occurs. In the only example where RUE was calculated in sweet corn (Stone *et al.*, 2001a) a simple linear relationship was used and no indication of a decrease in RUE post-silking observed.

There is less support for a low RUE during maize establishment (Sinclair and Muchow, 1999) but Giaufrett *et al.* (1991) calculated an RUE of 0.45 g DM MJ^{-1} in the establishment phase and 1.35 g DM MJ^{-1} subsequently. In other studies with maize the low establishment RUE has been related to leaf stage (Plenet *et al.*, 2000a) and LAI (Sierra *et al.*, 2003).

It is possible that this low RUE is an artefact of the methods used. In most cases daily RI is not directly measured but calculated from GLAI using an assumed extinction coefficient (Giauffret *et al.*, 1991; Sierra *et al.*, 2003). In this approach minor errors may accrue in RI from errors in predicted GLAI or k. Due to the small biomass and RI_{cum} values during establishment, any error in RI_{cum} may have a large effect on calculated RUE. In contrast RI was measured directly using linear quantum sensors and a low RUE was found during sunflower establishment (Gimenez *et al.*, 1994; Trapani *et al.*, 1992).

The reasons for lower RUE during maize establishment may also be that partitioning of dry matter to roots is greater during this establishment phase leading to an apparently reduced RUE. However, the data of Trapani *et al.* (1992) showed that when RUE was based on total crop DM a similar pattern occurred. It is also possible that during establishment the very low LAI means light saturation of the leaves occurs and therefore RUE is lower. This hypothesis is supported by the theoretical analysis of Sinclair and Horie (1989), which showed that at a LAI of 0.5 RUE was 1.19 g DM MJ^{-1}, but at LAI of 4.5 RUE was 1.38 g DM MJ^{-1} in rice. Conversely the C4 pathway in maize means light saturation is unlikely to occur in maize or sweet corn. An alternative hypothesis is that air temperatures in these studies may have been lower during establishment leading to reduced RUE. However, given the wide range of environments in which this has been reported, this is also unlikely. Another possibility is that the initial three leaves in maize have a lower photosynthetic capacity (e.g. Thiagarajah *et al.*, 1981).

In summary it is unclear whether or why RUE in maize is lower during establishment. But it is more likely to be of importance in warm season crops (e.g. *Zea mays*) grown in cool temperate environments. This is because the low temperatures mean that crop development is

slower compared with tropical areas and consequently the RI_{cum} at any development stage is greater in these cool environments. Therefore the initially low RUE during establishment is more obvious in these experiments.

2.3.2.2 Nutrient effects

Nutrient supply can also affect crop RUE. However, the literature has predominantly reported the effect of N on crop yield being associated with reduced RI and not in RUE (Sinclair and Muchow, 1999). Using a crop simulation model Jamieson and Semenov (2000) showed that the effects of N on wheat yield could be reproduced by assuming that N was constant per unit of leaf area and hence RUE was constant.

The evidence suggests that this is an over simplification in maize. Both RI and RUE are reduced by N deficiency in maize (Muchow, 1994; Muchow and Davis, 1988; Muchow and Sinclair, 1994) with RUE effects related to specific leaf N (SLN). SLN is the concentration of N reported on a leaf area basis. For example, maize RUE increased by 1.1 g DM MJ^{-1} for every 1 g N m^{-2} increase in SLN, within the range between 0.55-1.55 g N m^{-2} (Muchow and Davis, 1988). This lower value seems to be the approximate limit for N stressed maize grown in both the field (Chapman and Barreto, 1997; Muchow, 1994; Muchow and Davis, 1988) and controlled environments (McCullough *et al.*, 1994). Additional N limitations lead to a decrease in leaf so that a SLN of ~0.55 g m^{-2} is maintained. Field (Muchow and Sinclair, 1994) and theoretical analyses (Sinclair and Horie, 1989) have shown that this relationship between RUE and SLN is due to the close relationship between photosynthesis and SLN. I am unaware of literature where sweet corn RUE has been linked to variations in N supply. However, given the similarities between maize and sweet corn a similar response could be expected.

There are comparatively few studies examining the effects of P on RUE. The small literature set has provided inconclusive results. In maize P fertiliser had no effect on RUE and reductions in grain yield were due to RI (Plenet *et al.*, 2000a). In contrast a limited P supply reduced RUE in wheat (Rodriguez *et al.*, 2000) and sunflower (Colomb *et al.*, 1995).

2.3.3 Photosynthesis

2.3.3.1 Light curves

Leaf photosynthetic rates depend principally on the radiation incident at the leaf surface. As light levels increase so does the rate of photosynthesis up until a point when the photosynthetic apparatus becomes light saturated and hence no further increases are possible. This response is frequently described using a non-rectangular hyperbola (Marshall and Biscoe, 1980a, b; Thornley and Johnson, 2000) (Equation 2.4).

$$Pg = \frac{1}{2\theta}\left[\alpha \times I + P_{\max} - \left[\alpha \times I + P_{\max}\right]^2 - 4\theta \times IP\max\right]^{\frac{1}{2}}\ ] - Rd$$

Equation 2.4

Where P_g is the rate of gross photosynthesis (μmol CO_2 m^{-2} s^{-1}), I is the irradiance incident on the leaf (μmol m^{-2} s^{-1} PPFD), α is the initial slope of the hyperbola (μmol CO_2 μmol $PPFD^{-1}$), θ is a dimensionless parameter defining the degree of curvature, P_{max} is the theoretical maximum rate of photosynthesis (μmol CO_2 m^{-2} s^{-1}), and Rd is the rate of dark respiration (μmol CO_2 m^{-2} s^{-1}) at 0 μmol m^{-2} s^{-1} PPFD.

All the variables in this equation have relevant biological meaning. However, the value of light saturated photosynthesis (P_{max}) is of principal interest in explaining RUE. C3 species obtain light saturation of photosynthesis at around 1000 μmol PPFD m^{-2} s^{-1} (e.g. Peri *et al.*, 2002a), whereas full sunlight may have a maximum value of 2000 μmol PPFD m^{-2} s^{-1} (McKenzie *et al.*, 1999). Therefore it is appropriate to examine P_{max} as a biologically meaningful variable in C3 species. In contrast, in C4 crops light saturation rarely occurs under full sunlight and therefore examining P_{max} values is unrealistic. As a consequence many studies with maize have used values such as P_{2000} (photosynthesis rate at 2000 μmol PPFD m^{-2} s^{-1}) to examine photosynthesis. This approach will be used in this review. Furthermore there is a wide range of units in which photosynthetic rates are reported, but in this review they have all been converted to a standard unit of μmol CO_2 m^{-2} s^{-1}.

There is a strong relationship between RUE and maximum leaf photosynthesis (Sinclair and Muchow, 1999). Any factor that increases leaf photosynthetic rate increases RUE. This accounts for the higher RUE in maize (1.6-1.7 g DM MJ^{-1}) compared with C3 crops, such as wheat (1.4 g DM MJ^{-1}) (Kiniry *et al.*, 1989; Sinclair and Muchow, 1999). Values of P_{2000} as high as 50 μmol CO_2 m^{-2} s^{-1} have been reported for field grown maize (Dwyer *et al.*, 1989), whereas values of P_{max} in C3 species are much lower e.g. 27.4 μmol CO_2 m^{-2} s^{-1} in cocksfoot (*Dactylis glomerata*) (Peri *et al.*, 2002a) and 19.2 μmol CO_2 m^{-2} s^{-1} in wheat (Marshall and Biscoe, 1980b). In a growth chamber, sweet corn ('Golden Bantam') P_{2000} was 48 μmol CO_2 m^{-2} s^{-1} (Ward and Woolhouse, 1986). Maize and sweet corn photosynthetic rates are of a similar magnitude, which is expected because the principal difference between the crops is in the endosperm (Laughnan, 1953) and not the photosynthetic system.

2.3.3.2 Relationships with environment and physiology

Many aspects of the environment affect maize photosynthesis. These include acclimation to light (Ward and Woolhouse, 1986), temperature (Tollenaar, 1989a; Tollenaar *et al.*, 1991) and chilling stresses (Aguilera *et al.*, 1999; Long *et al.*, 1983; Stirling *et al.*, 1993; Ying *et al.*, 2002). The latter two are of paramount importance in a cool temperate climate such as Canterbury. Maximum photosynthetic rate of *Zea mays* occurs at a mean growth temperature of ~27°C (Figure 2.4) (Tollenaar, 1989a). Supra-optimal temperatures also limit photosynthesis. However, maize photosynthetic rates are relatively stable (~40-50 μmol CO_2 m^{-2} s^{-1}) until temperatures exceed 38°C (Crafts-Brandner and Salvucci, 2002). R_d will also increase with increasing temperature and this may have important effects on RUE (Loomis and Amthor, 1999). Maize and sweet corn crops in Canterbury experience air temperatures that are generally at or below the optimum for net leaf photosynthesis. Therefore high temperature limitations of photosynthesis will not be considered further.

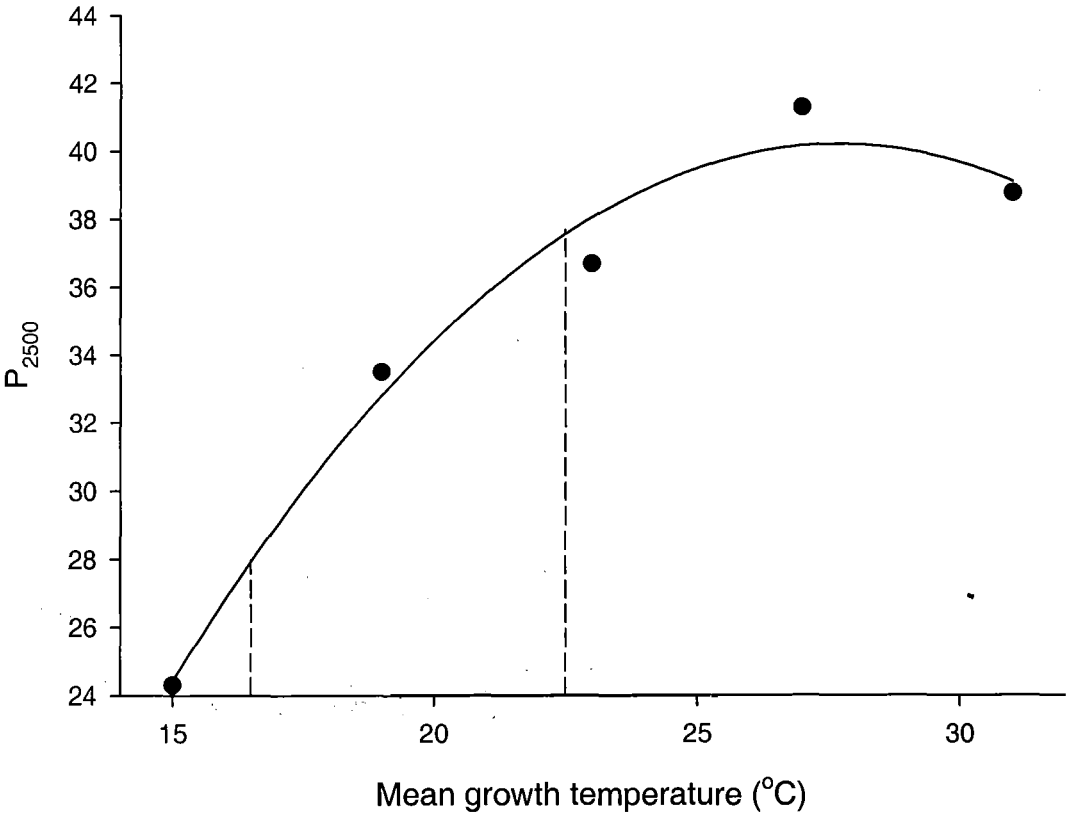

Figure 2.4 Maize photosynthetic rate (μ mol CO_2 m^{-2} s^{-1}) at 2500 μ mol PPFD m^{-2} s^{-1} (P_{2500}) grown in a controlled environment study at five constant temperatures (15-31°C) (Adapted from Tollenaar, 1989a). Fitted equation is y = -35.1 (±11.6) + 5.44 (±1.05) x – 0.098 (±0.023) x^2 (R^2= 0.96). The dotted lines represent the range in monthly mean maximum air temperatures at Lincoln, between November and April.

Mean air temperatures in Canterbury during the sweet corn growing season (November – April) are generally less than 27 °C, which often restricts photosynthesis. However, optimum temperatures appear to be different for RUE and photosynthesis. Maize RUE declined at <20°C (Section 2.3.2.1) whereas photosynthesis declined at <27°C (Figure 2.4). The magnitude of reduction in photosynthesis with decreasing air temperature is small and quadratic so the effect on RUE was not apparent until temperature fell to 20°C. Using the

equation from Figure 2.4 at 20°C, P_{2500} is still 85% of its maximum, whereas at 12°C P_{2500} is only 40% of maximum. Theoretical analyses (Sinclair and Horie, 1989) have indicated that it takes a large decrease in leaf photosynthetic rate to have noticeable effect on RUE.

Additionally, early and late in the season, air temperatures frequently fall to extreme low temperatures (~0 °C) for short periods, which will lead to chilling stress limiting photosynthesis. Long *et al.* (1983) showed that maize subjected to a 6-hour chill period at 10°C had a rate of photosynthesis at 1500 μ mol PPFD m^{-2} s^{-1} at 60% of its maximum, but when the chilling temperature was 5°C this fell to 50%.

The age of an individual maize leaf also influences photosynthesis with maximum rates at the time of full leaf expansion (Dwyer and Stewart, 1986b; Dwyer *et al.*, 1989; Stirling *et al.*, 1994). These results all indicate that to minimise experimental variation associated with leaf age, measurements of maize and sweet corn photosynthesis should be obtained from the youngest fully expanded leaf and adjusted for temperature.

2.3.3.3 N and P responses

A number of examples in the literature show maize leaf photosynthetic rates were reduced when N supply was limited. This includes examples from controlled environments (Khamis *et al.*, 1990; McCullough *et al.*, 1994) and field studies (Muchow and Sinclair, 1994). There is unlikely to be a difference in the response of photosynthesis to N supply in sweet corn and maize.

P deficiency reportedly decreases maize leaf photosynthetic rates (Jacob and Lawlor, 1991, 1992; Usuda and Shimogawara, 1991, 1992) which contradicts the results for RUE (Plenet *et al.*, 2000a). However, the photosynthesis results were obtained from experiments with young

plants grown in controlled environment rooms. For example, Jacob and Lawlor (1991) grew maize at low light levels (350-400 μ mol m^{-2} s^{-1} PPFD), and measured photosynthesis on the third true leaf. Similarly Usuda and Shimogawara (1991) grew maize in a controlled environment and measured photosynthesis between 9 and 24 days after planting. Clearly this is not representative of field conditions where PPFD may be as high as 1900 μ mol m^{-2} s^{-1} (Peri *et al.*, 2002b), and maize crops may have 16 to 20 or more leaves (Robertson, 1994). In addition, the intensity of P deficiency imposed during laboratory studies of P supply on leaf photosynthesis is most likely to be far greater than that encountered in a field situation. For example, at the end of a P starvation experiment with maize (Mollier and Pellerin, 1999) obtained a P concentration of 1 mg g^{-1}, whereas at a similar development stage in a maize field crop that had not received P fertiliser Plenet *et al.*, (2000b) found a P concentration of ~3 mg g^{-1}. Controlled environment measurements are useful for understanding the mechanisms of photosynthesis, but limited in their ability to approximate conditions in a field crop. There is little relevant data for leaf photosynthetic rates in response to P fertiliser in field grown maize or sweet corn.

2.3.4 Harvest index

The final part of Equation 1.1 is HI. This is a coefficient derived from the proportion of economic to total biomass (Donald, 1962; Donald and Hamblin, 1976). In grain crops such as maize, HI is the grain DM as a proportion of crop DM. However, in sweet corn the way in which HI is expressed depends on the end use of the crop. For a processed sweet corn crop HI is the kernel DM as a proportion of total crop DM, whereas for the fresh market HI is the proportion of ear DM. Therefore it is difficult to make comparisons based on HI in sweet corn unless the harvestable fraction is clearly defined. For comparison with maize, for which there is a wealth of literature, HI in this review has been confined to focus on kernel yield.

Maximum maize HI is 0.5 (Birch *et al.*, 1999; Hay, 1995; Muchow, 1990; Sinclair, 1998; Stone *et al.*, 1999). However, HI is not a consistent proportion of crop DM throughout the duration of the crop. There is an approximately linear increase (with days) in HI that begins following a lag period after silking. Muchow (1990) determined that HI increased by 0.015 day^{-1} following a lag period of 3.5 days after maize silking. Whereas, Birch *et al.* (1999) found that these parameters were cultivar dependent. These analyses ignore the effect of temperature, which at sub-optimal values limits the increase in HI. Using a sensitivity analysis Wilson *et al.* (1995) showed that the linear HI increase was maximum at temperatures above 19°C but then fell linearly to be 0 at 8°C.

Similar increases in HI also occur in sweet corn. In a study with two sweet corn hybrids, (Stone *et al.*, 2004) HI (based on ear as a proportion of total crop biomass) increased by 0.089 $°Cd^{-1}$ (T_b=5°C). HI based on grain yield is generally lower than that found in maize. For example, reanalysis of the data of Stone *et al.* (2001a), from different irrigation treatments in Canterbury, and Rogers *et al.* (2000), from different sowing dates in Hawkes Bay, showed that kernel HI (i.e. kernel DM as a proportion of total crop DM) was 0.24 in 'Challenger' sweet corn harvested at canning maturity (72% kernel moisture) (Figure 2.5). This reflects the fact that sweet corn is harvested during the period of linear increase in HI and before the maximum potential HI has been reached.

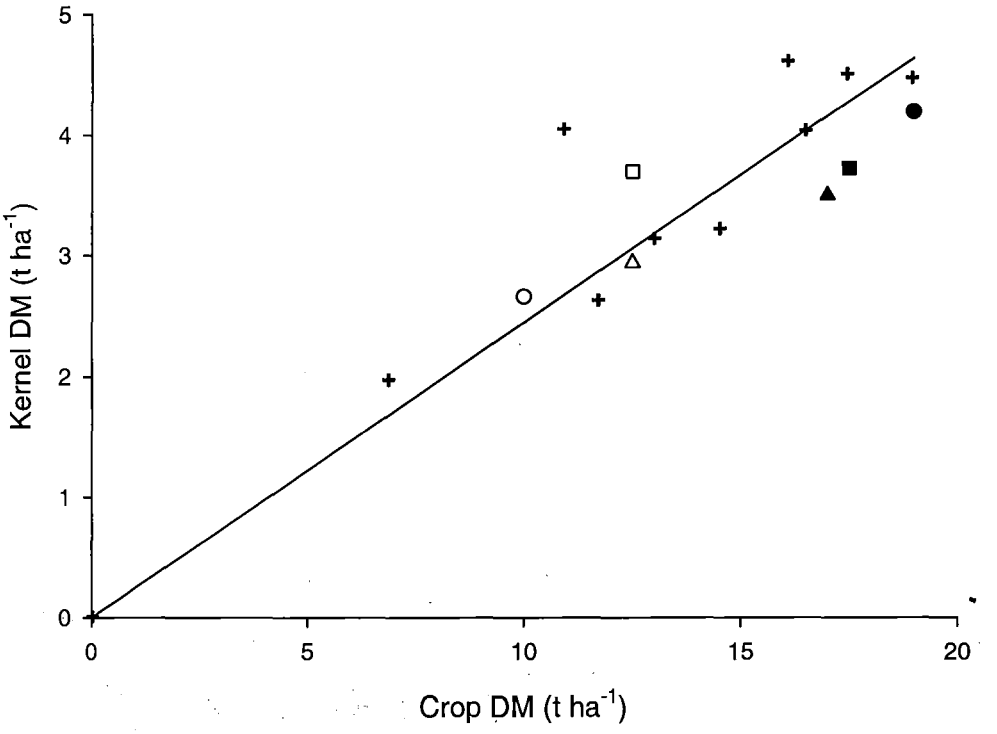

Figure 2.5 Reanalysis of relationship between total crop biomass and kernel DM in 'Challenger' sweet corn grown from Stone *et al.* (2001a) and Rogers *et al.* (2000). Symbols represent different drought treatments imposed on the crop. (●) Fully irrigated (PSMD 90mm), (○) Full drought (PSMD 403 mm), (■) Mild early drought (PSMD 132mm), (□) Severe early drought (PSMD 254 mm), (Δ) Mild late drought (PSMD 237 mm), and (▲) Severe late drought (PSMD 363 mm) (Stone *et al.*, 2001a); and crosses (+) represent different sowing dates (21 September 1999- 20 January 2000) at Hawkes Bay (Rogers *et al.*, 2000). Regression (constrained to pass through 0,0) is $y = 0.24\,x$ $R^2 = 0.80$. Data are taken from Figure 4 and Figure 6 of Stone *et al.* (2001a) and kernel DM data is calculated from kernel FM assuming that kernel moisture is 72%; and the sowing date data (Rogers *et al.*, 2000) was kindly provided by P.J. Stone.

N and P limitations may reduce crop yield by reducing total crop biomass (the product of RI and RUE in Equation 1.1), HI, or both. Maize grain yield under limited N and P supply are

reduced primarily by a decrease in crop biomass and then by a decrease in HI. Plenet *et al.* (2000a) found a HI of 0.45-0.48 in grain maize yields that ranged from 10.6-14.2 t ha^{-1} in response to three fertiliser P rates. However, Muchow (1988b) found differences in final HI of grain maize in response to N fertiliser ranging from 0 to 420 kg N ha^{-1}. The rate of linear increase in HI was constant and the maximum crop HI was only reduced when no N was applied. In contrast, grain yield was decreased with reduced N over the full range of N treatments. The primary cause of grain yield decrease was the reduced crop biomass. This was consistent with Muchow (1994) who showed HI was decreased under N deficiency (0 c.f. 240 kg N ha^{-1}) across a range of sowing dates but the effect of N deficiency on crop biomass was proportionately greater than on HI. Furthermore the smallest HI's were associated with the lowest grain yields (Figure 2.6) indicating that HI was unaffected until levels of extreme stress i.e. when grain yields were < 60 g $plant^{-1}$. Therefore the lack of response in crop HI to P observed by Plenet *et al.* (2000a) may relate to the high yields achieved of 10.6-14.2 t ha^{-1} which relate to grain yields per plant of 142-172 g $plant^{-1}$ even in the lowest P treatment.

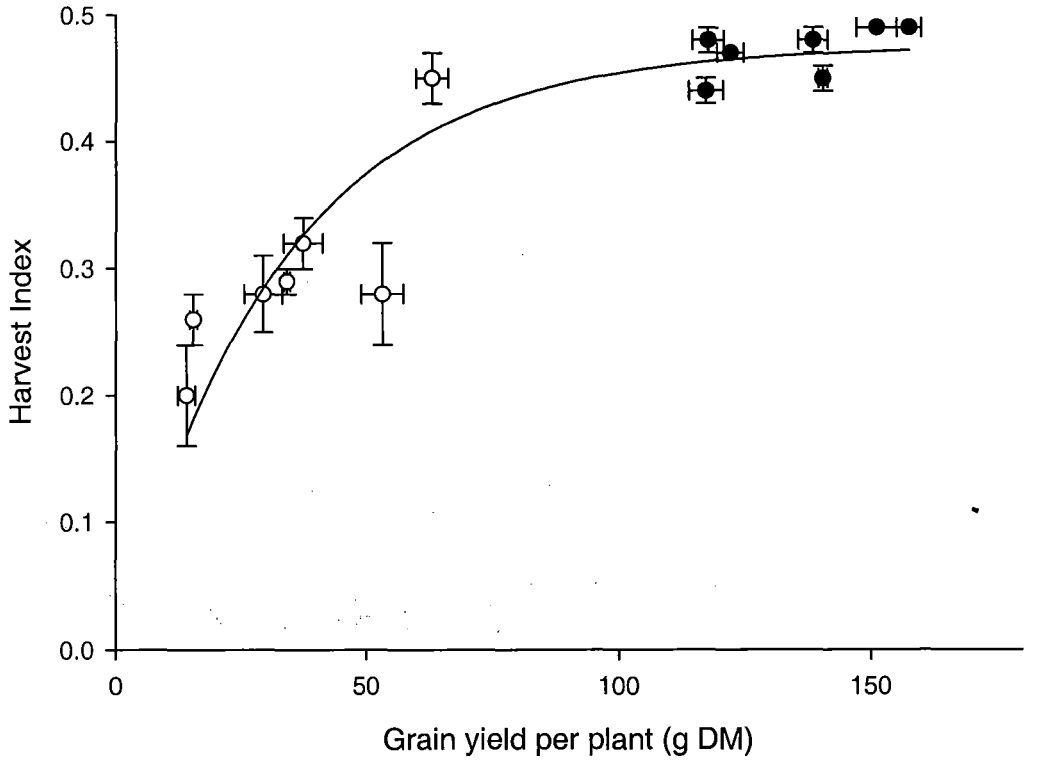

Figure 2.6 Harvest index and grain yield per plant of grain maize grown at seven sowing date-location combinations with either 0 (○) or 240 (●) kg N ha^{-1} applied. (Adapted from Muchow, 1994). Error bars represent s.e.

2.3.5 Yield components in maize

In maize and sweet corn it is also possible to describe grain yield using yield components. Grain yield in maize is the product of individual grain mass and the number of grains per unit area. Any factor that reduces grain yield may affect one or both of these variables. Some experiments where these variables have been reported as a factor of some physiological stress are summarised in Table 2.3. Linear relationships between total grain yield and either grain weight or grain number were used to examine their importance in determining yield.

Table 2.3 Reanalysis of selected references outlining the extent to which grain yield in maize and sweet corn is related to either the grain number per plant, or individual grain weight. The relationships were examined using least squares regression.

Reference	*Treatment*	[a] *R^2 grain number*	[b] *R^2 grain weight*	*Grain yield range t ha^{-1}*
(Plenet *et al.*, 2000a)	P	0.065	0.931	10.6-14.2
(Jamieson *et al.*, 1995)[c]	Drought	0.13	0.61	~10-12
(Stone *et al.*, 2001a)[d]	Drought	0.52	0.69	Unknown [e]
(Muchow, 1994)	N	0.99	0.90	0.99-11
(Barbieri *et al.*, 2000)	N	0.61	0.36	6.1-13.3

[a] R^2 of least squares linear regression between grain yield (g m^{-2}) and grain number (m^{-2})
[b] R^2 of least squares linear regression between grain yield (g m^{-2}) and grain weight (g)
[c] Regression analyses were presented by the authors in this paper. All other data were reanalysed here.
[d] Study with sweet corn in response to drought stress. All results were based on FM (72% kernel moisture); kernels per ear is used instead of kernel yield; and kernel number ear^{-1} was used instead of kernel number m^{-2}.
[e] crops were harvested at fresh corn canning maturity (72% kernel moisture), before physiological maturity and therefore direct comparisons with other data is not possible.

Grain yield in response to P was more closely related to grain mass than grain number (Plenet *et al.*, 2000a). A similar result was found for drought stress (Jamieson *et al.*, 1995). However, when N was limiting yield the grain number became of greater or equal importance (Barbieri *et al.*, 2000; Muchow, 1994). In the single example with sweet corn the yield per ear was more closely related to kernel mass than kernel number, in water stress treatments (Stone *et al.*, 2001a). There is probably no specific difference between the stresses that leads to this divergent pattern. It is more likely related to the timing of stresses. In an extensive literature review of source: sink relationships in grain maize, Borras *et al.* (2004) used a bi-linear regression analysis to conclude that any stress that reduces post-anthesis (silking) assimilate supply will reduce individual grain mass of maize. Whereas the number of kernels per plant or kernels per ear was closely related to the growth rate in a period bracketing silking (Andrade *et al.*, 2002). This implies that for experiments where grain weight was the most

important determinant of maize grain yield (Jamieson *et al.*, 1995; Plenet *et al.*, 2000a; Stone *et al.*, 2001a) assimilate production and remobilisation were limiting, and the potential seed number (determined around silking) was less affected. When grain number was of equal or greater importance, assimilate supply around silking was also reduced.

The range in grain yield was also an important factor determining whether grain number or grain mass limited yield. With grain yields <60 g plant^{-1} changes in maize grain yield caused by stress were primarily determined by individual grain mass. Whereas, for grain yields > 60 g plant^{-1}, decreases in grain number were increasingly important (Figure 2.7). This relationship may be a result of the timing of individual environmental stresses. A severe stress, that will have a more deleterious effect on grain yield, will generally occur earlier in crop development when grain number is determined. Therefore, grain number will be more affected than individual grain mass. A less severe stress will usually only act later in crop development when grain filling is occurring. Therefore individual grain mass will be most affected

This relationship is similar to the relationship between crop HI and grain yield (Figure 2.6), in that crop HI changes are of little importance at grain yields > 60 g plant^{-1}. This implies that mild stresses reduce yield by limiting crop biomass, leading to smaller grains but with a constant crop HI. However, as stresses become more acute crop HI also decreases. That is because the potential number of grains per unit area is reduced.

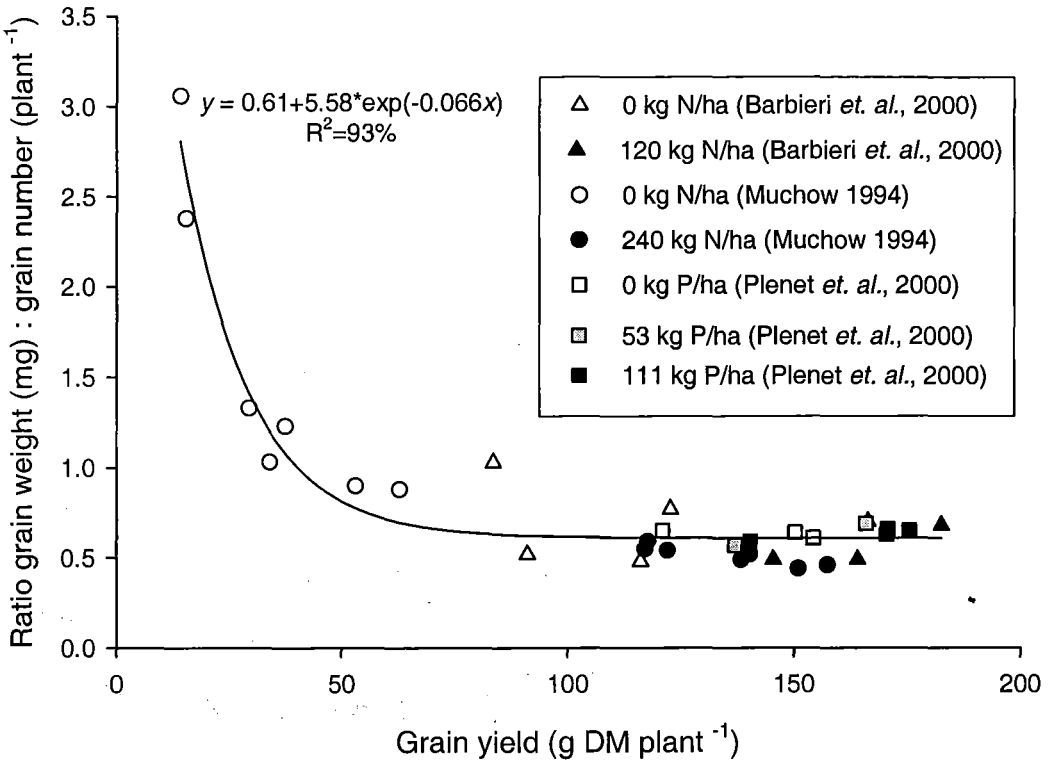

Figure 2.7 Relationship between ratio of grain weight (mg) to grain number (plant $^{-1}$) and grain yield (g DM plant^{-1}) in grain maize from a range of N and P treatments (Adapted from Barbieri *et al.*, 2000; Muchow, 1994; Plenet *et al.*, 2000a).

Similar mechanisms probably operate in sweet corn in response to both N and P stress. However, it would be impossible to directly compare results with maize (Figure 2.7) with those in sweet corn crops. This is because sweet corn is harvested before grains have reached their maximum size, and therefore the ratio of individual grain mass to grain number is likely to be substantially less in sweet corn.

2.4 Sweet corn quality

For some markets the quality of sweet corn is important in determining crop value (Rogers *et al.*, 2000). Specific quality variables that are important will be determined by the end use of the crop. For fresh markets the visual appearance of ears is of paramount importance in determining customer quality (Tracy, 2001).

Other quality parameters are also important for different end uses. These include kernel toughness, colour, sugar levels, and aroma. Many of these chemical components of quality such as aroma (Wong *et al.*, 1995; Wong *et al.*, 1994) and sugar levels (Faleiros *et al.*, 1996; Kaldy and Freyman, 1973) are related to fertiliser applications. However, hybrid choice (Laughnan, 1953; Michaels and Andrew, 1986) and harvest time (Culpepper and Magoon, 1924; Hwi *et al.*, 2001; Magoon and Culpepper, 1926; Michaels and Andrew, 1986) seem to be more appropriate methods of manipulating sugar levels in sweet corn.

Visual appearance of ears is important in determining fresh market sweet corn quality (Tracy, 2001). The important variables include the yield structure within an ear, i.e. kernels per row, rows per ear, kernels per ear, and individual kernel mass (Section 2.3.5); but also the ear dimensions, i.e. ear length, diameter, and the unfilled tip length. These variables have been almost exclusively examined in sweet corn, but are comparatively unimportant in maize.

Some of these quality parameters have been measured previously in response to management variables. Stone *et al.* (2001a) showed that moisture stress (PSMD 90- 403 mm) decreased kernels per ear and the number of kernels per row but did not affect ($p<0.05$) the number of rows per ear or the individual kernel mass of 'Challenger' sweet corn.

Sweet corn ear dimensions are sensitive to sowing date (Rogers *et al.*, 2000) and plant spacing (Rogers and Lomman, 1988). In Hastings, New Zealand, Rogers *et al.* (2000) showed that every 10 day delay in sowing resulted in a 0.86 t ha^{-1} decrease in total crop biomass and a 1 mm decrease in ear length of three sweet corn hybrids. The primary (1°, upper most ear) ear diameter was constant (~50 mm) until the final sowing date (20 January) when it decreased by 5-10 mm. These results imply that both ear diameter and ear length were under strong genetic control and were maintained at relatively constant size. However, for the last sowing date ear diameter declined markedly due to a massive reduction in total crop biomass.

The unfilled tip length is a major quality component. In the study of Rogers *et al.* (2000) unfilled tip length (~10%) was relatively constant until November sowing dates. Following this there was a major reduction in the unfilled tip length of some hybrids. For hybrid XP1029 it fell to ~60% unfilled at the final sowing date while in 'Challenger' (used in this research) it was unaffected. Rogers and Lomman (1988) showed that as the sweet corn plant population increased the unfilled tip length increased in four hybrids. These results show changes in sweet corn yield structure and ear dimensions in response to crop management. However, in all cases treatments also affected crop biomass, implying a source limitation on ear dimensions. These relationships warrant further investigation and will be evaluated in the present study.

Some limited studies of sweet corn quality responses to N and P fertiliser treatments have been reported. However, most of these studies are of limited value because only one or a few quality components are reported, and in some cases analyses have been site and season specific (Section 2.2). A rare exception was Stone *et al.* (1998a) where the response to either

0 or 250 kg N ha^{-1} and a range of populations was examined in 'Challenger' sweet corn. Applying 250 kg N ha^{-1} did not affect the unfilled tip length but did increase the individual kernel mass. This response was consistent over a range of populations from 30 000 to 140 000 plants ha^{-1} and hence a range of potential total crop biomass from 7-15 t DM ha^{-1}. This implies that the stress was most severe during kernel filling and that assimilate production around silking did not limit the number of kernels formed.

Sanchez *et al.* (1991) and Sanchez *et al.* (1989) both showed that P fertiliser did not affect ear length but affected both ear diameter and unfilled tip length in sweet corn. However, the response was variable between and within studies. In Florida two spring sown sweet corn crops (21 February and 24 March) had an increase in ear diameter of 6.7-9.5 mm with 100 kg P ha^{-1} broadcast compared with the 0 kg P ha^{-1} crop. For an autumn sown crop there were no differences in ear diameter between P treatments (Sanchez *et al.*, 1991). Similarly unfilled tip lengths decreased by ~22 mm with 100 kg P ha^{-1} broadcast onto spring sown sweet corn but only 9 mm for the autumn sown crop (Sanchez *et al.*, 1991).

A more mechanistic method would be to establish a relationship between yield per plant and ear diameter or unfilled tip length. The reanalysis in Figure 2.8 shows that there were clear relationships between these two variables and yield per plant. Both ear diameter and unfilled tip length are strongly related to kernel yield per plant. The greatest plant yields were associated with the lowest unfilled tip length and the greatest ear diameter. The exponential relationship of unfilled tip length with kernel yield per plant (Figure 2.8a) indicated that kernel yields > 300g FM $plant^{-1}$ would not greatly decrease the unfilled tip length because the unfilled tip length was approaching 0 mm. For ear diameter the response was logarithmic (Figure 2.8b). Specifically, decreases in kernel yield from 350 to 100 g FM $plant^{-1}$ resulted in

an approximately linear decrease in ear diameter from 48-42 mm. Further decreases produced more marked reductions with a diameter of 34 mm at a mean kernel yield of 10.3 g FM plant^{-1}. Any effect of P fertiliser on sweet corn ear quality is likely to be associated with a decrease in kernel yield per plant.

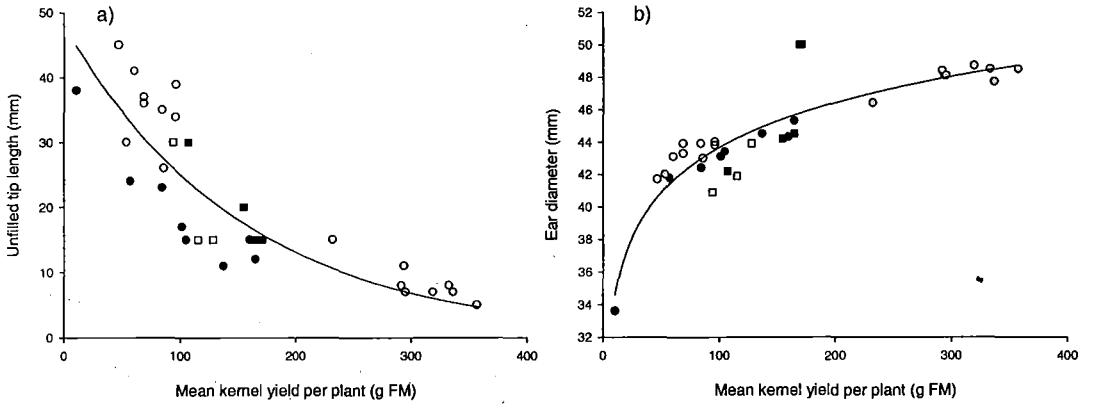

Figure 2.8 Relationships between unfilled tip length (mm) (a) and ear diameter (mm) (b) with kernel FM yield per plant of sweet corn from a range of P fertiliser treatments grown at five site-season combinations. Symbols denote sweet corn grown on: Pahokee muck soil sown on either 21 February (●) or 7 October 1989 (○), Terra Ceia muck soil sown on 24 March 1989 (◦) (adapted from Sanchez *et al.*, 1991); or Pahokee muck soil in two years (■,□) (actual years not given) (adapted from Sanchez *et al.*, 1989). All sites were in Florida. Regression equations are (a) y = 48 (±4.3) * exp [-0.0065 (±0.0009) x] R^2=72%; and (b) y=25.3 (±1.77) + 4.0 (±0.36) *ln* x R^2= 78%.

In contrast, Bar Yosef *et al.* (1989) found no differences in sweet corn ear diameter with a range of P fertigation treatments (0.04-1.29 mmol P m^{-3}). However, in this experiment mean kernel yields per plant were all between 290 and 390 g FM plant^{-1} where little change in ear diameter is expected (Figure 2.8b).

2.5 Reproductive development

In this section the focus is on the key phenological stages (emergence, silking and maturity) in sweet corn and their responses to environment, N and P supply.

From an agronomic perspective phenological development is important because growers are interested in how much and when yield will be produced. Secondly phenological sub-models are an important part of crop simulation in that they determine how the plant responds to a set of environmental variables (Hodges, 1991).

A specific reason for examining sweet corn development is the need to schedule production and the subsequent processing of raw product (Brooking and McPherson, 1989; Olsen *et al.*, 1993; Wurr *et al.*, 2002). To achieve this crop management (i.e. sowing date and hybrid) is manipulated, and a semi-mechanistic understanding of crop development is used to estimate the effects on sweet corn maturity (Brooking and McPherson, 1989; McPherson and Brooking, 1989).

The timing of crop maturity in a marginal climate will also determine the risks of crop production. The risks of both sweet corn and maize failing to mature before the first autumn frost in Canterbury were quantified by Wilson and Salinger (1994) and Wilson *et al.* (1994). For both sweet corn and maize risks were minimised by using early sowings and short maturity hybrids. In Canterbury the risk of sweet corn maturity failure was ~0 when an early maturity hybrid (1100 °Cd, T_b = 6°C) was sown on 15 October. This risk increased substantially to 0.6 or 60% for a late maturity hybrid (1400 °Cd) sown on 30 November (Wilson and Salinger, 1994). Any factor that delays the date of maturity will increase the risk of sweet corn crop failure.

2.5.1 Temperature and photoperiod

In the absence of environmental stress (e.g. water and nutrient limitations) crop development depends on temperature and to a lesser extent photoperiod. To quantify this heat units, also known as growing degree days or thermal time (Tt), and photo thermal time have been used (e.g. Weir *et al.*, 1984 in wheat). In sweet corn the photoperiod effect on development is minimal in Australia (Olsen *et al.*, 1993) and New Zealand (Brooking and McPherson, 1989). Therefore in this section the effect of photoperiod on sweet corn development will be disregarded.

Temperature effects on crop development are quantified using Tt (°Cd). This is the sum of daily mean temperatures (T_{mean}) minus a base temperature (T_b) except that where T_{mean} is less than T_b the value is 0 (Equation 2.5). This analysis assumes that the response to temperature is linear. In reality there is an optimum temperature (T_{opt}) above which development decreases. T_{opt} has been reported as 34°C in maize (Kiniry and Bonhomme, 1991) and 30-34°C in sweet corn (Olsen *et al.*, 1993). In cool temperate regions such as Canterbury maximum air temperatures rarely exceed 34°C. Therefore in this review the discussion will focus on the linear sub-optimal response, between T_b and T_{opt}.

$$Tt = \sum_{i=1}^{n} T_{mean} - T_b ; (T_{mean} > T_b)$$

$$Tt = \sum_{i=1}^{n} 0 ; (T_{mean} \leq T_b)$$

Equation 2.5

Using Tt to quantify development is less variable than chronological days. This is because at warm temperatures the rate of crop development is more rapid than at cooler temperatures. An

example of this is Wilson and Salinger (1994), where the coefficient of variation for planting to maturity of sweet corn from 10 sowing dates was between 7.6 and 10.6% based on days or 1.5 and 3.9% based on thermal time.

Accurately defining T_b is an essential step in using Tt to quantify crop development (Shaykewich, 1995). This can be achieved in a number of ways, including minimising the variation in days, minimising the variation in Tt, or from extrapolating a T_b from a regression of development rate on temperature (Yang *et al.*, 1995). All methods work by statistically optimising a value of T_b, which might be quite different from the physiological value (Bonhomme, 2000). Furthermore, the Tt concept uses a linear function to approximate a curvilinear response to temperature (between T_b and T_{opt}). Therefore the value of T_b obtained to some extent depends on the range of temperatures used to derive it (Bonhomme, 2000).

An abundance of literature has defined T_b for both maize and sweet corn (Appendix 1).The T_b for both maize and sweet corn is between 5 and 10°C, and most likely 6-8°C for the emergence to silking period. By contrast, the range of T_b from silking to maturity is 0-8°C. For the latter the data of Muchow (1990) provides compelling evidence that T_b = 0°C in maize as it is based on a linear regression between development rate and temperature. However, the limitations of these data must also be acknowledged, in that the regression is based on a temperature range from 25-32°C, meaning that a large degree of extrapolation to a T_b of 0°C was required.

Calculating Tt based on T_{mean} assumes that T_{min} is always greater than T_b. Where the maximum daily temperature is less than T_b this is not a problem as this means that Tt is 0°Cd. However, when the maximum temperature is greater than T_b but the minimum is less the use

of T_{mean} will underestimate development. This is because the temperatures below T_b will have a negative impact on the predicted daily development, whereas in reality they will have a value of 0 °Cd. To overcome this difficulty a method is commonly used where a modified sine curve is used to calculate Tt at three hourly intervals, which are then integrated over a day (Jones and Kiniry, 1986). This method is most important for a C4 crop (high T_b), such as sweet corn, produced in a temperate climate such as Canterbury, where T_{min} frequently falls below T_b.

2.5.2 Fertiliser effects

There are examples in the literature where both N and P fertiliser have affected maize and sweet corn development. However, few of these examples have studied development in a mechanistic way and quantified it using Tt. Furthermore, many of these examples have disregarded the delay in development with nutrient deficiencies.

Maturity was delayed by 9 days without N fertiliser from 98.8 days with 420 kg N ha^{-1} to 107.8 days with 0 kg N ha^{-1} in a maize crop grown in N.T., Australia (Muchow, 1988a). The major cause of this was a 7.7 day delay in the emergence to silking period. Similarly, in an experiment with 7 sowing date×site combinations, Muchow (1994) showed a mean 5.5 (±1.14) day delay in silking in a maize crop receiving 0 kg N ha^{-1} compared with a crop receiving 240 kg N ha^{-1}. However, the period from silking to crop maturity was accelerated by 2.3 (±1.45) days when no N was applied. This implies that there was an intrinsic link between development and growth. The delay in silking was not caused by a direct physiological change in development but a lack of crop growth to express development. Although the silks were ready to appear crop growth rate meant that their emergence was delayed when no N was applied.

These data are also consistent with data for sorghum (*Sorghum bicolor* L. Moench). Sorghum development prior to anthesis is similar to that in maize. Sinclair *et al.* (1996) reported the results of three experiments and showed that anthesis in sorghum could be delayed by up to 20 days when N was limiting growth in one experiment. However, data from the other two experiments showed that mean daily temperature close to either T_{opt} or T_b limited the magnitude of this response.

P supply also affects the phenological development of grain maize. Plenet *et al.* (2000b) reported that flowering was delayed by 2-4 days (33-65°Cd; T_b=8°C) in a maize crop receiving no P fertiliser compared with 93kg P ha^{-1} yr^{-1} for three seasons. In situations of extreme P stress the delay can be even greater. Sorghum flowering and physiological maturity have been shown to be delayed by 33-34 days in a 0 kg P ha^{-1} crop compared with a 10 kg P ha^{-1} crop (Sahrawat *et al.*, 1995).

In a two year study with sweet corn grown with (13kg N ha^{-1} and 19 kg P ha^{-1}) or without (0 kg N and P ha^{-1}) starter fertiliser, Swiader and Shoemaker (1998) found that silking occurred ~ 4.5 days later in the unfertilised crops compared with the fertilised one. Swiader and Shoemaker (1998) also showed a linear regression between seedling dry mass (32 days after planting) and days to silking, showing that larger seedlings reached silking faster than smaller seedlings. Early crop growth was related with subsequent development rates.

2.6 Semi-mechanistic modelling of maize growth and development

2.6.1 Potential

As outlined previously, these individual crop processes can be linked together to form a simulation model of crop growth and development. These mechanistic models are a set of quantified hypotheses about how crops grow and interact with the environment (Section 1.2). There have been many models published regarding the growth and development of maize for example CERES maize (Jones and Kiniry, 1986) and hybrid maize (Yang *et al.*, 2004). However, many of the aspects of crop growth and development examined in the preceding sections have been integrated into a simple model of maize crop growth and development (Muchow *et al.*, 1990). This model uses 13 equations to integrate the effects of temperature and solar radiation on maize growth and development (Figure 2.9). The framework encapsulated in this model is used as a basis for examining sweet corn yield in this thesis. The usefulness of this model in studying maize yields is a function of its simplicity. In contrast, other models contain many calculations that account for various aspects of crop growth. For example Hybrid-maize (Yang *et al.*, 2004) contains 28 modifiable crop parameters. These complex models may sometimes give a closer simulation of observed results, but much of their power and utility is lost in their complexity. In fact Sinclair and Seligman (2000) stated that "the scientific merit of a modelling study is likely to follow from its 'leaness' rather than from its complexity".

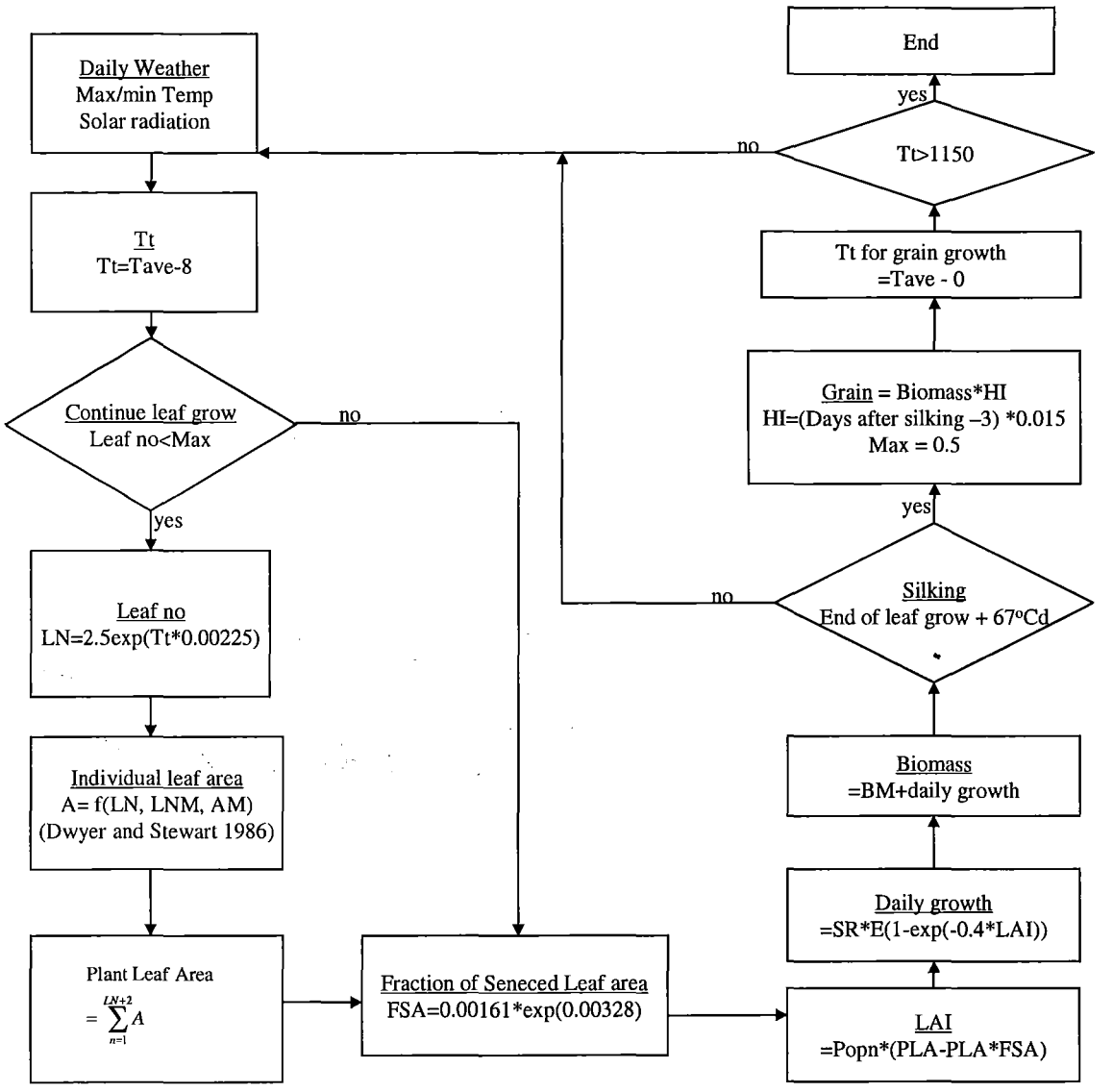

Figure 2.9 Flow diagram representation of a simple semi-mechanistic growth and development model for grain maize (adapted from Muchow *et al.*, 1990).

The model of Muchow *et al.* (1990) assumes that water and nutrients are non-limiting. However, the framework is sufficiently robust that a number of modifications can be introduced to accommodate these stresses. To summarise, the model works by first calculating PLA. This is calculated as the sum of areas of the current fully expanded leaves and the next two leaves (accounting for leaves that have not fully expanded yet). Individual leaf area is calculated from a bell-shaped curve (Dwyer and Stewart, 1986a) (Section 2.3.1.2) and leaf number is an exponential function of Tt after emergence (T_b= 8°C) (Section 2.3.1.1).

Next, FSA is calculated from an exponential function with Tt (Section 2.3.1.3). Plant population, PLA and FSA are then used to calculate GLAI for a given day (Section 2.3.1.4). Light interception is then calculated using an extinction coefficient of 0.4 and daily growth is calculated from radiation interception using a constant RUE. RUE is 1.6 g DM MJ^{-1} during vegetative growth and 1.2 g DM MJ^{-1} from 500 °Cd after silking (to account for N remobilisation) (Section 2.3.2). Crop biomass is calculated as the sum of the previous day's biomass and the daily growth of the current day. Grain biomass is then calculated as the crop biomass multiplied by the HI (maximum of 0.5), which increases by 0.015 per day from 0 at 3 days after silking (Section 2.3.4). Silking is deemed to occur at 67°Cd after the expansion of the final leaf. These calculations continue until 1150 °Cd (T_b = 0°C) after silking when the crop reaches maturity (Section 2.5.1).

This model was successful in simulating maize grain yields across 21 site-seasons in sub-tropical and tropical environments. Residual mean squared deviation (RMSD) was 96.3 g grain m^{-2} (Muchow *et al.*, 1990). Furthermore the data of Rogers *et al.* (1999) showed that this framework could be used to examine sweet corn with only minor modifications. One limitation of this framework in sweet corn is that it will not explain quality changes. However, the quality responses are linked to crop biomass and could therefore be incorporated (Section 2.4).

This framework ignores the effects of water limitations. Muchow and Sinclair (1991) successfully incorporated the effects of water stress on crop growth by relating RUE and leaf development to the fraction of transpirable soil water available. This modified model simulated maize grain yields across a range from 0 to 773 g m^{-2}.

The original model was developed in tropical and subtropical environments. In a cool temperate environment in Lincoln, Canterbury, New Zealand it did not accurately simulate either development or grain yield. The RMSD for grain yield was 372 g grain m^{-2} or 49% of mean observed grain yield and for maturity the RMSD was 59 days or 34% of observed days from sowing to maturity (Wilson *et al.*, 1995). Wilson *et al.* (1995) included a number of modifications to the model, which dramatically improved simulations of both grain (RMSD=103 g m^{-2}) yield and maturity. These included a modified phenology model and a modified biomass accumulation method; essentially RUE was decreased by temperatures below 16 °C; and a modified grain growth model where HI increase was limited at temperatures below 19 °C.

2.6.2 N and P responses

There are a number of semi-mechanistic crop growth models for a variety of crops that have included the effects of nutrient stresses on growth and yield. These include maize (Jones and Kiniry, 1986) and wheat (Jamieson *et al.*, 1998a). However, virtually all these models have concentrated extensively on the effects of N. This is not surprising given the over-riding importance of N on crop growth processes (McLaren and Cameron, 1998).

The model reviewed in Section 2.6.1 (Muchow *et al.*, 1990) has also been modified to simulate the effects of N stress on maize grain yield (Sinclair and Muchow, 1995). These modifications simulated N uptake as the minimum of either potential uptake, determined by Tt, or the soil available N determined by a soil N budget (Sinclair and Amir, 1992). Daily N uptake was then partitioned to biomass components, with 60% going to leaves. Leaf area was modified so that a minimum canopy SLN of 0.55 was maintained (2.3.1.2). SLN was able to increase above this value, and RUE was linearly related to SLN. RUE was 0.72 g DM MJ^{-1} at 0.55 g N m^{-2} and reached its maximum value of 1.6 g DM MJ^{-1} at a SLN of 1.35 g N m^{-2}

(Section 2.3.2.2). Functions were also included to simulate N remobilisation during grain filling. This simple set of modifications successfully encapsulated the key physiological drivers of maize growth under limited N supply and successfully simulated (R^2=96%) maize grain yield responses to N supply ranging from 100 to 1100 g m^{-2} (Muchow and Sinclair, 1995). This model analysis is more useful than the simple asymptotic yield response curve (Sections 2.2.1 and 2.2.2) in that it shows how yield was restricted under limited N supply. Because the model is physiologically based results can then be extrapolated to other environments with more confidence. One limitation of this model is that it did not include any changes in crop development (section 2.5.2) or leaf appearance (Section 2.3.1.1) associated with N supply.

In contrast to the models of N response in grain maize, there are few if any, where mechanistic responses to P have been studied. There are some where uptake of P from the root zone has been studied (Jones *et al.*, 1984; Probert, 2004), but few where mechanistic whole crop responses have been examined. Two notable exceptions are APSIM (Kinyangi *et al.*, 2004; Probert, 2004) and DSSAT (Daroub *et al.*, 2003) where maize responses to P have been simulated. However, in these models the emphasis has been on the uptake of soil P, and only crop yield responses were presented. The mechanisms within the crop that reduced yield in P limiting conditions were not well documented. This is an area where a mechanistic understanding of the effects of P supply on crop yield may be useful in examining P responses across sites and seasons for both maize and sweet corn.

2.7 Conclusions

- The literature shows that sweet corn yield is reduced with limited N and P supply. These responses have generally been studied with site-season specific statistical analyses that have been related to either applied fertiliser or nutrient supply.
- Understanding the individual processes that determine sweet corn yield is an important goal for optimising production practices. The variables of principal interest are: leaf appearance rates, the area of individual leaves and senescence determining GLAI and RI_{cum}; RUE and photosynthesis; HI and biomass partitioning; and quality relationships with sweet corn yield.
- The response of these individual processes to key environmental (including temperature, solar radiation, water and N supply) variables has generally been well studied.
- These individual processes have been successfully integrated into a simple growth model of maize that can predict potential yields, water limited yields, and N limited yields well. Given the similarities between sweet corn and maize this framework is likely to apply to sweet corn.
- However, quantitative data regarding the individual processes that respond to a limited P supply in maize and sweet corn are sparse and warrant further examination.

Chapter 3. Materials and methods

3.1 Introduction

This research included five experiments with 'Challenger' sweet corn (*Zea mays*) grown in Canterbury, New Zealand in 2001/2002 and 2002/2003. This chapter outlines the site, experimental and agronomic details of these experiments, including long term and seasonal weather data, crop husbandry and measurements. Additional methods and measurements specific to each results section are reported in subsequent chapters.

3.2 Site description

3.2.1 Soil type

The experimental area is known locally as 'Simpson's' block, and is located at AgResearch Lincoln (43° 62'S and 172° 44'E), Canterbury, New Zealand. The soil is a Templeton fine sandy loam, moderately deep phase, with small areas of an Eyre shallow fine sandy loam (Cox, 1978). Using the 'Revised New Zealand Soil Classification' (Hewitt, 1998), the Templeton soil is classed as a Mottled, Immature, Pallic Soil; and the Eyre as an Immature, Orthic, Brown Soil (Hewitt, 1995). Both soils are 'Udic Ustochrepts' using the USDA soil taxonomy system (Soil-Survey-Staff, 1999). Both soils have low P retention (0-30%) (McLaren and Cameron, 1998).

Both soils were formed from alluvium and loess from greywacke parent material and are well drained. Typically this Templeton soil consists of 460-600 mm of fine sandy loam above sandy gravels; and the Eyre shallow fine sandy loam consists of 250-460 mm of fine sandy loam over gravels (Cox, 1978). A full description of these soils was given by Cox (1978),

with additional soil physical data available from Webb *et al.* (2000) and Webb (2003). The available water holding capacity (AWC) of these soils under pasture is 150-200 mm for the Templeton and 100-150 mm for the Eyre (Webb, 1989).

3.2.2 Fertility

The site had not been limed or fertilised for at least 15 years prior to the experiments and was dominated by brown top (*Agrostis capillaris*). A soil test taken on 14 May 2001 indicated low soil P (Olsen P = 6 $\mu g\ ml^{-1}$), low pH (5.7), and low sulphate sulphur (2 ppm) values (Table 3.1).

Table 3.1. Soil test results from 14 May 2001 for the field site at Lincoln, Canterbury, New Zealand, and recommended soil nutrient levels for sweet corn (Clarke *et al.*, 1986) and maize (Cornforth and Sinclair, 1984) crops.

Nutrient	pH	P	K	S SO_4	Mg	Ca	Na
Unit	-	$\mu g\ ml^{-1}$	MAF QT[1]	ppm	MAF QT	MAF QT	MAF QT
Soil test value	5.7	6	12	2	14	4	5
ppm[2]		6.5	237	2	69	495	25
Recommended for sweet corn	5.3-6.8	30-35[3]	8[4]	-	-	-	-
Recommended for maize	-	-	-	5	5	-	-

[1] Ministry of Agriculture and Fisheries, quick test results (Cornforth, 1980).
[2] Parts per million; conversion assumes soil Bulk density of 0.92 (data not shown).
[3] For Low P retention soils (0-40%).
[4] For loam soil.

3.2.3 Long term climate

The environment is classified as cool and temperate but is characterised by frequent soil moisture deficits with an annual rainfall of 640 mm. Monthly rainfall exceeds potential

evapo-transpiration from September to April in most years (Table 3.2). The long term mean (LTM; 1975-2000) temperature measured at Broadfields' meteorological station, located approximately 3 km east of the site, is 11.5 °C but reaches a maximum of 16.7 °C in January and a minimum of 6.2 °C in July.

3.2.4 Seasonal weather

The two experimental seasons had contrasting prevailing weather patterns. The 2001/02 season (November-April) had monthly mean temperatures 0-1.5 °C cooler than the LTM with 9% less solar radiation (Table 3.2). The season was also 34% wetter than the LTM, with 125 mm of rainfall in January, which is double the LTM. Evapo-transpiration was also 10% lower than the LTM between November and April (Figure 3.1a). In the 2002/03 season solar radiation exceeded the LTM by 4%, but mean temperatures were 0.6 °C cooler than the LTM (Table 3.2). There was a 'freak' chilling event on 27 December 2002, when the air temperature fell to a minimum of 0.4 °C overnight. During this season, rainfall and potential evapo-transpiration rates were similar to the LTM (Figure 3.1b).

Table 3.2. Long term mean (LTM, 1975-2000) and actual measurements of accumulated total solar radiation (SR) and mean, minimum and maximum temperatures from November to April in 2001/2002 and 2002/2003 recorded at the Broadfields' Meteorological Station, Canterbury, New Zealand.

	Total solar Radiation ($MJ\ m^{-2}$)			Mean Temp (°C)			Min Temp (°C)			Max Temp (°C)		
	LTM	01/02	02/03	LTM	01/02	02/03	LTM	01/02	02/03	LTM	01/02	02/03
Nov	625	572	598	12.9	13.2	12.2	7.9	9.3	7.1	18.3	17.8	17.6
Dec	696	613	780	15.4	15.5	15.3	10.2	10.8	9.6	21.0	20.7	21.0
Jan	689	553	685	16.7	16.0	16.0	11.5	12.2	10.7	22.2	20.2	21.6
Feb	536	484	625	16.4	14.9	15.9	11.3	11.0	10.3	21.8	19.2	21.8
Mar	440	493	476	14.8	15.0	15.2	9.7	9.3	10.8	20.0	21.3	20.4
Apr	290	253	256	12.1	11.5	10.4	6.9	7.7	5.4	17.3	16.0	15.2
Mean Nov-Apr	546	495	570	14.8	14.4	14.2	9.6	10.1	9.0	20.1	19.2	19.6

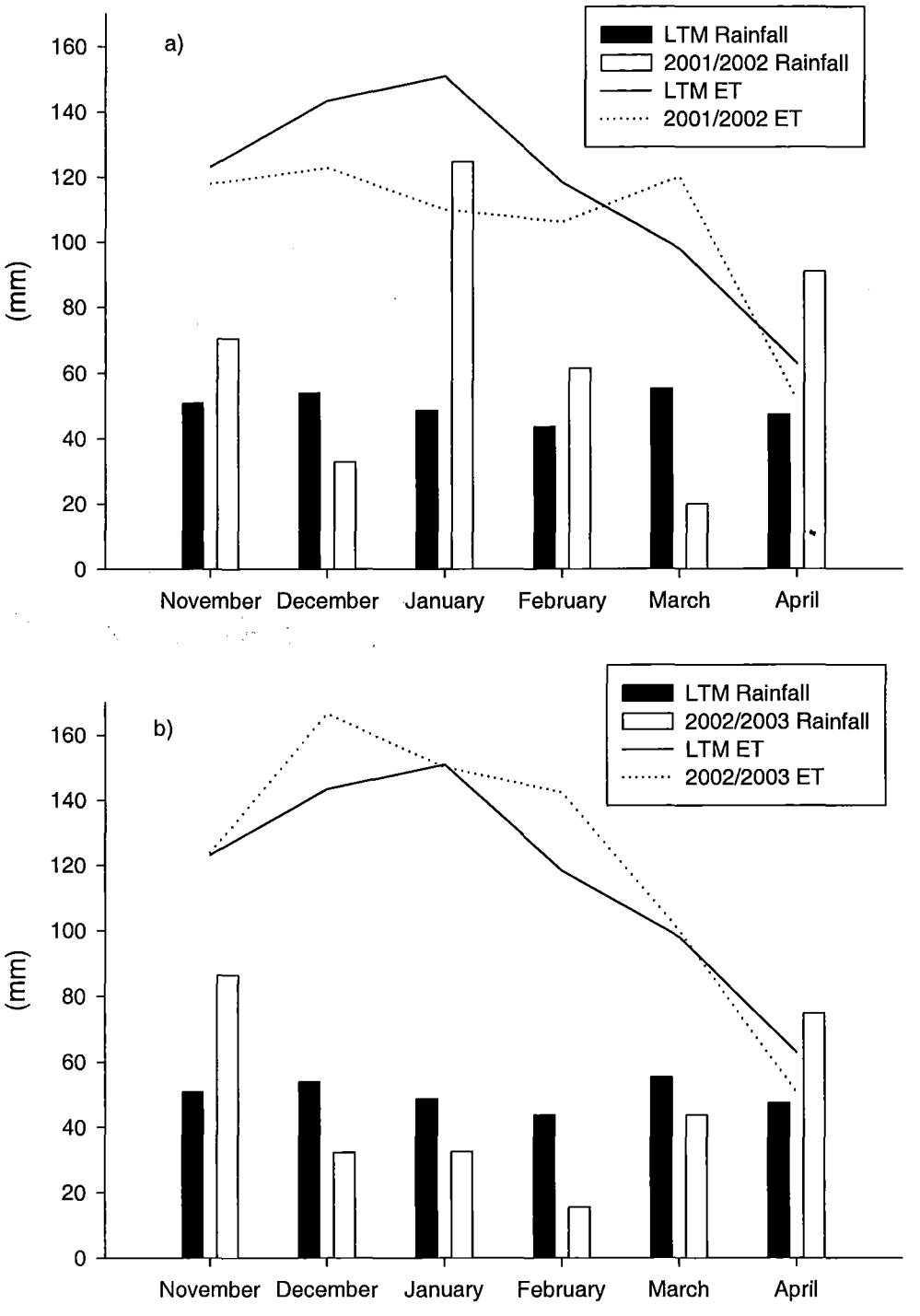

Figure 3.1. Long term mean (LTM, 1975-1991) and actual measurements of rainfall and Penman potential evapo-transpiration (ET) from November to April in: 2001/2002 (a) and 2002/2003 (b), recorded at Broadfields' meteorological station, Canterbury, New Zealand.

3.3 Details of Experiments 1 and 2, 2001/02

Three experiments were sown in a common 0.5 ha paddock in the 2001/02 season.

3.3.1 Site preparation and basal fertiliser dressings

On 11 September 2001 a number of small trees (<2.5 m in height) that covered 15-20% of the site were removed. On 12 September 2001, the site (for all experiments) was sprayed with glyphosate at 1.4 kg ai ha^{-1} with a wetting agent, 'Freeway', to remove resident pasture. The experimental site was rotary-hoed and rolled on 20 September 2001. Following this the area was ploughed on 21 September 2001 and top worked with a rota-crumbler on 25 September 2001.

A basal application of 35 kg S ha^{-1} as potassium sulphate (PS; 0,0,40,7) was applied to the entire area on 3 October 2001 using a tractor and spreader. N and P fertiliser was also applied to the area. These were applied at a common rate except where different N and P treatments were established in Experiments 1 and 2 (Section 3.3.2). The common rate of N applied was 300 kg N ha^{-1}. This was hand applied as calcium ammonium nitrate (CAN; 26,0,0,0) in three split applications of 100 kg N ha^{-1} on 15 October, 20 December 2001 and 16 January 2002. The common rate of P applied was 200 kg P ha^{-1}. This was hand applied as triple super phosphate (TSP; 0,21,0,0) in two split applications of 100 kg P ha^{-1} on 6 and 14 October 2001. The first applications of TSP (6 October 2001) and PS (3 October 2001) were incorporated into the soil to an approximate depth of 150 mm using a rota-crumbler on 8 October 2001. The application of CAN (15 October 2001) and the second application of TSP (14 October 2001) were not incorporated due to rainfall (2.6 mm) on 16 October.

3.3.2 Fertiliser treatments and experimental design

3.3.2.1 Experiment 1. Phosphorus response

Experiment 1 was sown on 25 October and consisted of five rates of P (0, 50, 100, 150, and 200 kg P ha^{-1}) as TSP (Table 3.3) in a randomised complete block design with three replicates. These plots had only received basal dressings of CAN and PS as outlined in Section 3.3.1 (i.e. no basal TSP). Plots were 4.9m wide (7 rows) and 10 m long (49 m^2).

Table 3.3. Experiment 1 rates (kg nutrient ha^{-1}) and application dates of phosphorus, nitrogen and sulphur applied to 'Challenger' sweet corn at Lincoln, Canterbury, New Zealand 2001/2002.

	Fertiliser					
	Phosphorus (kg ha^{-1})		Nitrogen (kg ha^{-1})			Sulphur (kg ha^{-1})
Date	6/10/01	14/10/01	15/10/01	20/12/01	16/1/02	3/10/01
P0	0	0	100	100	100	35
P50	25	25	100	100	100	35
P100	50	50	100	100	100	35
P150	75	75	100	100	100	35
P200	100	100	100	100	100	35

3.3.2.2 Experiment 2. Nitrogen response

Experiment 2 was sown on 1 November and consisted of five rates of N (0, 45, 90, 180, and 300 kg N ha^{-1}) as CAN (Table 3.4) in a randomised complete block design with three replicates. For these plots only basal dressings of TSP and PS had been applied previously (Section 3.3.1). Plots were also 4.9 m wide (7 rows) and 10 m long (49 m^2).

Table 3.4. Experiment 2 rates (kg nutrient ha^{-1}) and application dates of phosphorus, nitrogen and sulphur applied to 'Challenger' sweet corn crops at Lincoln, Canterbury, New Zealand 2001/2002.

	Fertiliser					
	Phosphorus (kg ha^{-1})		Nitrogen (kg ha^{-1})			Sulphur (kg ha^{-1})
Date	6/10/01	14/10/01	15/10/01	20/12/01	16/1/02	3/10/01
N0	100	100	0	0	0	35
N45	100	100	30	0	15	35
N90	100	100	60	0	30	35
N180	100	100	80	40	60	35
N300	100	100	100	100	100	35

3.4 Details of Experiments 3 and 4, 2002/2003

3.4.1 Site preparation and basal fertiliser dressings

Following the completion of the 2001/02 growing season corn stalks were cut at ground level and removed from the plots. In preparation for the 2002/03 season the site was sprayed with glyphosate at a rate of 1.1 kg ai ha^{-1} with a wetting agent 'Freeway' on 29 August 2002 to remove weeds. The plots were then rotary-hoed using an SEP on 6 and 7 November 2002 in preparation for planting and to incorporate additional second season applications of TSP and CAN.

In the 2002-2003 season Experiments 3 and 4 were sown on 7 November 2002. For both of these experiments a basal dressing of 300 kg N ha^{-1} was also applied in three applications on 29 October 2002, 7 January 2003, and 11 February 2003 as CAN. The soil test taken on 10 June 2002 (Appendix 2) indicated that the soil pH had dropped to 5 across the paddock and the sulphate S level was still marginal at 4 ppm. To alleviate these gypsum (0,0,0,22), at a rate

of 35 kg S ha^{-1} was applied to the plots on 30 October 2002 and burnt lime, ($Ca(OH)_2$) was applied to the experimental area at a rate of 3.2 t ha^{-1} on 25 October 2002, using a tractor and spreader.

3.4.2 Experiment 3: Low P response

Experiment 3 was a repeat of Experiment 1 (Table 3.3) but with an additional 0, 0, 10, 20, or 40 kg P ha^{-1} as TSP hand applied on 31 October 2002 to the P0, P50, P100, P150, and P200. Thus the plots became P0, P50, P110, P170, and P240 treatments respectively, with the value indicating the total applied P over the two years.

3.4.3 Experiment 4: High P response

Experiment 4 included an additional 40, 60, 80, 120, or 180 kg P ha^{-1} as TSP hand applied on 31 October 2002 to the N300, N180, N90, N45, and N0 treatments from Experiment 2 (Table 3.4). These plots had all received a basal dressing of 200 kg P ha^{-1} in 2001/02. Thus, they became treatments P240, P260, P280, P320 and P380, with the value indicating the total applied P over the two years. These plots all received 300 kg N ha^{-1} in 2002/03 so that N was not limiting growth.

In 2002/03 there was a range of crops that had received 0, 50, 110, 170, 240, 260, 280, 320 and 380 kg P ha^{-1} (combined across two seasons) (Table 3.5). Crops that had received 240 kg P ha^{-1} were present in both Experiments 3 and 4. These were used as check crops, to see if the yield response was different, in subsequent analyses (Section 4.2.2.1).

Table 3.5 Total and seasonal P application rates (kg P ha^{-1}) to Experiments 3 and 4 at Lincoln, Canterbury, New Zealand 2001/2002 and 2002/03.

Total kg P ha^{-1} (2001/2002 + 2002/03)	*kg P ha^{-1} (2001/02)*	*kg P ha^{-1} (2002/03)*
Experiment 3		
0	0	0
50	50	0
110	100	10
170	150	20
240*	200	40
Experiment 4		
240*	200	40
260	200	60
280	200	80
320	200	120
380	200	180

* The management of these crops was identical and they were used to cross-check the response to P supply in the two experiments.

3.5 Experimental management

3.5.1 Establishment of experiments

All plots were hand sown using jab planters (Plate 1). In the first season 'Challenger' sweet corn Lot No. ZME 1351 from Seminis seeds was used while lot 3272252/2 of 'Challenger' from Asgrow seeds was used in the second. Seeds were sown at an inter-row spacing of 700 mm and an intra-row spacing of 200 mm giving a target population of 71 000 plants ha^{-1}. Two seeds were planted at each position to a depth of approximately 50 mm and these were thinned (on 28 November 2001 and 19 December 2002) to produce uniform populations.

Due to variable emergence the actual attained plant populations were less than the target population. These populations were 58 800 plants ha^{-1} in Experiment 1, 56 680 plants ha^{-1} in Experiment 3, and 54 400 plants ha^{-1} in Experiment 4 (Appendix 3). Plant populations were not monitored in Experiments 2 and 3. The CV% in spacing between plants was 25% in Experiment 1, 23% in Experiment 3, and 29% in Experiment 4. In 2002/03 three plots had rows that had been 'missed' at sowing so these rows were replanted, using seed that had been imbibed at 20/30 °C for 3 days, on 28 November. These rows were not measured but were replanted to minimise the effect of variable interplant competition on the developing plants.

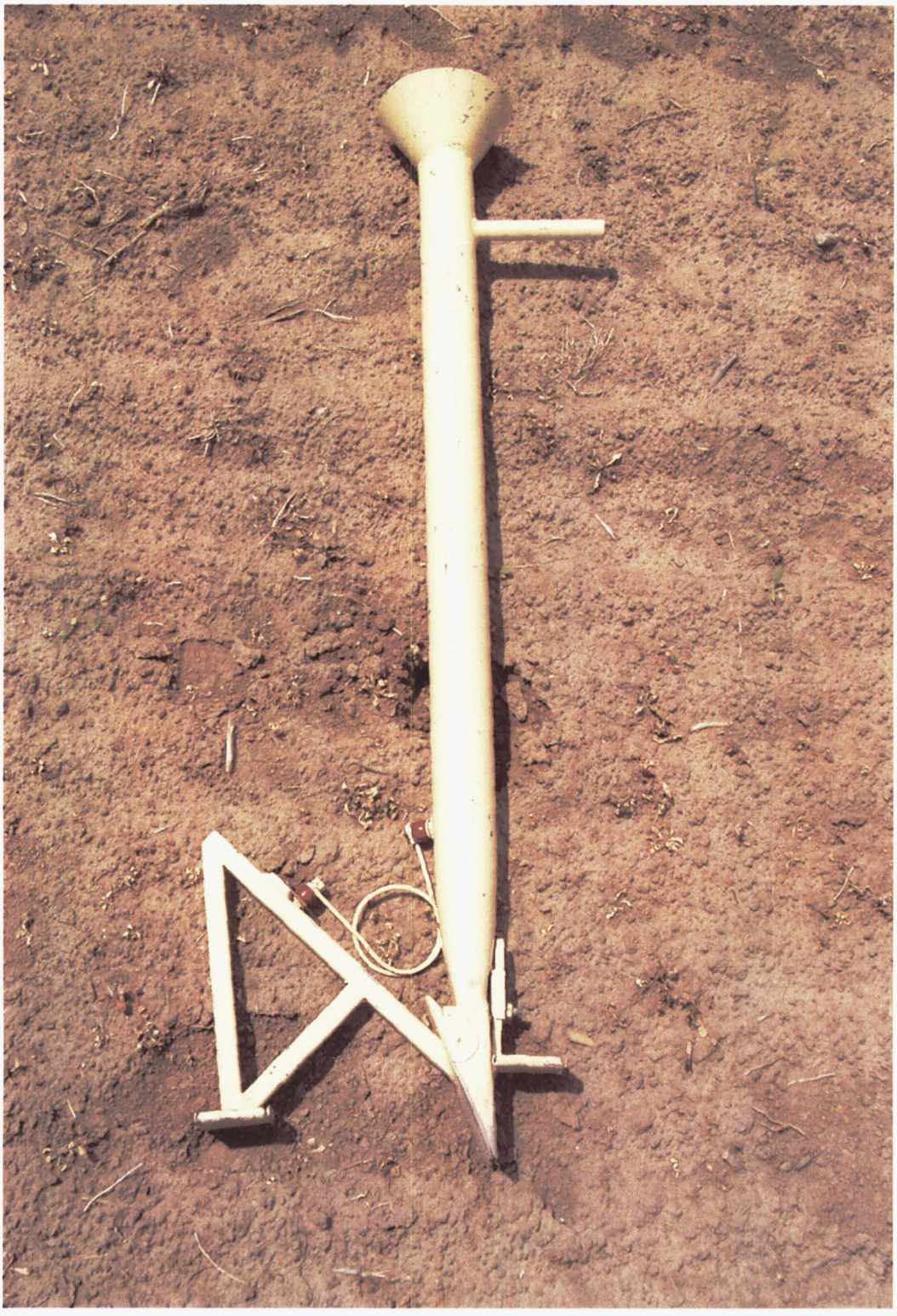

Plate 1 Jab planters used for sowing 'Challenger' sweet corn seeds in these experiments.

3.6 Agronomic management

3.6.1.1 Irrigation and water budget

Irrigation was applied using hand shift pipes arranged as sprinkler-sprinkler to cover each shift of approximately 10 m (the length of a plot). Irrigation was applied to avoid a critical deficit (Dc) calculated using the method of Stone *et al.* (2001a). This method assumed that the effective rooting depth increased at a rate of 1.3 mm (starting at 50 mm seed depth) per unit thermal time (Tt, T_b= 8°C) after sowing (Stone *et al.*, 2001b). It was assumed that total available water content (AWC) increased by 190 mm per metre of topsoil (Stone *et al.*, 2001a). The subsoil contained approximately 50% stones (Webb, 1989) and therefore this value was halved after the rooting depth reached 500 mm. Dc was considered to be 0.6 (Carcova *et al.*, 1998) of total AWC. A value of 0.5 is more usual for crops. However, Muchow and Sinclair (1991) indicated that leaf area development and transpiration did not decline until 0.7 fraction of transpirable water was used. Sensitivity analysis showed that the most important value in this approach was the fraction of AWC that was plant available, with depth to stones and AWC of soil having comparatively little effect on the maximum Dc calculated (Appendix 4).

Potential evapotranspiration (E) was calculated (Equation 3.1) for the two seasons using the method of Jamieson *et al.* (1995).

$$E = (1-\tau)E_p+E_s$$

Equation 3.1

Where E_p is the Penman evapotranspiration rate (French and Legg, 1979) taken from Broadfields' meteorological station; E_s is the soil evaporation rate; and τ is the proportion of crop ground cover. This was calculated from green area index (GAI) measurements taken periodically through the crop cycle, using a LAI 2000 canopy analyser (LI-COR Inc. Lincoln, USA) and Equation 3.2. GAI measurements from the fully fertilised crops in Experiment 1 and 4 were used to calculate τ in the two seasons.

$$\tau = e^{-kGAI}$$

Equation 3.2

E_s was calculated using a two-step process (Ritchie, 1972). It was assumed that in the two days following a soil-wetting event (>3 mm) evaporation was energy limited and therefore occurred at the potential Penman rate. Thereafter, the process became diffusion limited and was the minimum of either the potential rate or that calculated using Equation 3.3.

$$E_s = \varphi\, t^{1/2} - \varphi\, (t-1)^{1/2}$$

Equation 3.3

Where t is time after soil wetting event and φ is a soil diffusitivity constant, in this example a value of 4.2 mm day $^{-1/2}$ was used (Stone *et al.*, 2001a). E_s was then corrected for the proportion of bare soil by multiplying by τ, and added to E_p. A potential soil moisture deficit (PSMD) was calculated on a daily time step by subtracting E and adding any rain or irrigation applied. Positive values of PSMD indicate a surplus of moisture and were set to 0 mm on the assumption that drainage occurred. The soil profile was assumed to be at its drained upper

limit at crop emergence. The soil was likely to have been at or near this point based on winter rainfall.

In the 2001/02 season a limited degree of moisture stress occurred from 28 February 2002 (Figure 3.2). Therefore in the 2002/03 season longer (approx 1.8 m) risers were added to the pipes and irrigation throughout the whole crop cycle was possible and the crops requirement for moisture was fulfilled until harvest (Figure 3.2). The timing and amounts of irrigation applied are detailed in Table 3.6. The maximum PSMD calculated was 191 mm in 2001/02 season and 102 mm in 2002/03.

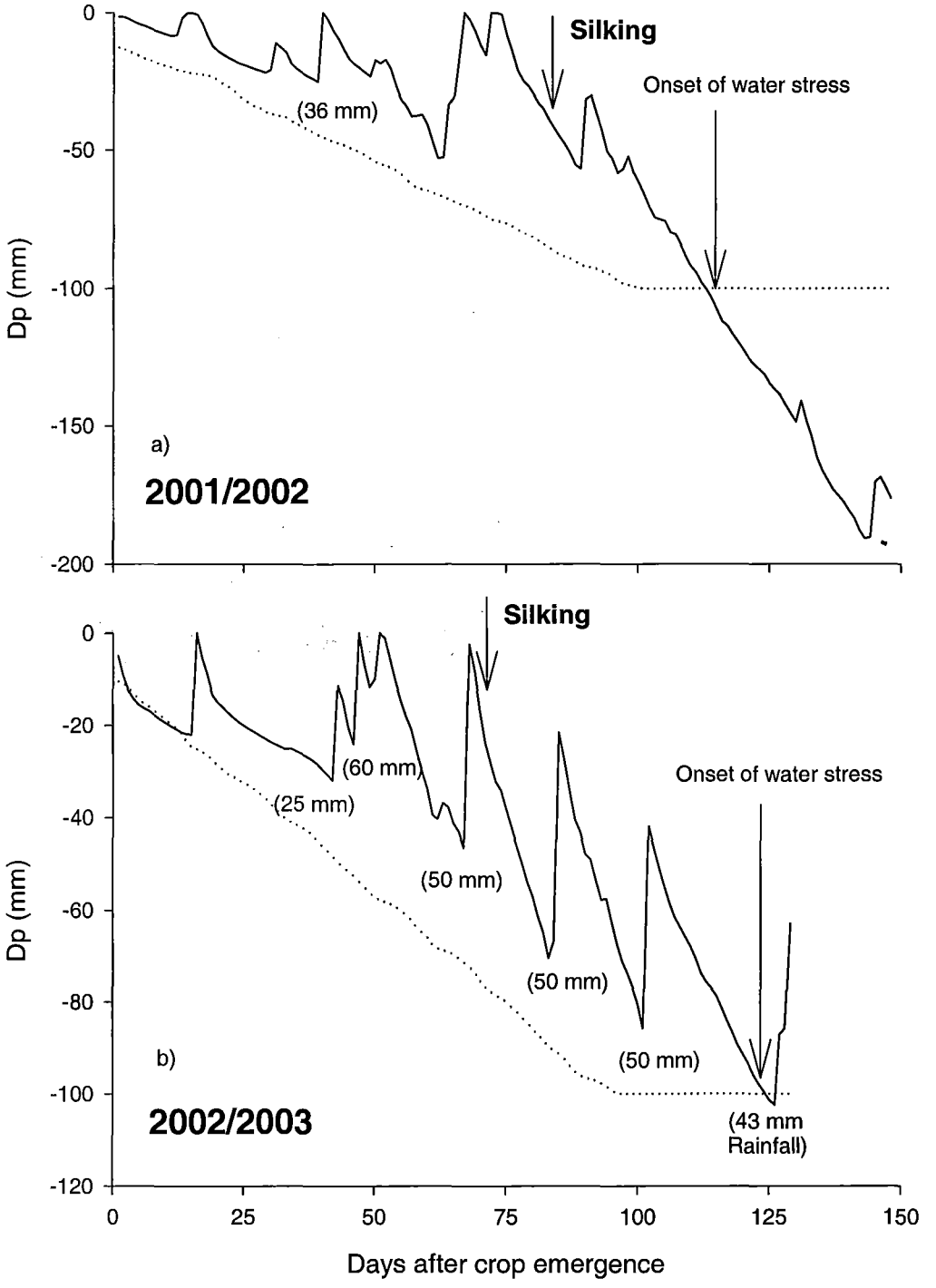

Figure 3.2 Water budget for fully fertilised 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/2002 (a) and 2002/2003 (b). Irrigation applications and the date of silking are marked. The dotted line represents the D_c, as calculated in Section 3.6.1.1.

Table 3.6. Dates and amounts of irrigation (mm) applied to 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand 2001/2002 and 2002/2003.

Date	17/12/01	4/1/03	8/1/03	14/2/03	29/1/03	43/03	Total (02/03)
Irrigation (mm)	36	25	60	50	50	50	235

3.6.1.2 Weed and pest control

Weeds were controlled using a combination of herbicides and hand removal. On 4 December 2001 plots were sprayed with Versatill (active ingredient 300 g L^{-1} clopyralid as amine salt) at a rate of 0.7 l ai ha^{-1} to control subterranean clover (*Trifolium subterraneum*). On 10 December 2001 broad-leaved docks (*Rumex obtusifolius)* were 'spot' sprayed using Asulox (active ingredient 400 g L^{-1} asulam as sodium salt). On 21 January 2002 plots were sprayed with a combination of 1.5 kg ai ha^{-1} of Atrazine and 0.4 kg ai ha^{-1} of Dicamba (as dimethylamine salt) using a 'knap-sack' and hood.

In the 2002/03 season Atrazine was sprayed at a rate of 1 kg ai ha^{-1} on 3 December 2002 to control a range of broad-leaved weeds. Additional weed control was obtained by removal with a hand hoe.

In the 2001/02 season Lannate (active ingredient 200 g L^{-1} methomyl) was sprayed on 12 November at a rate of 0.3 g ai ha^{-1} to prophylactically control Argentine stem weevil (*Listronotus bonariensis*) and greasy cutworm (*Agrotis ypsilon*) that can be a problem from sites recently out of pasture (Watson and Hill, 1985). In the 2002/03 season the crops were monitored for insect pests during emergence but no pesticides were required.

3.7 Measurements

3.7.1 Crop vegetative development

3.7.1.1 Leaf appearance

In Experiments 1 and 4 (P response), five contiguous plants per plot were marked. Counts of individual leaf tips and fully expanded leaves were made at 3-4 day intervals throughout the growing season. A leaf tip was considered to have appeared when it was clearly visible in the whorl of the plant. A leaf was defined as fully expanded when its ligule was visible (Plate 2). It was assumed at this point that the leaf had reached its maximum area. To aid identification the fourth and eighth leaf on marked plants were tagged using a spot of iridescent paint.

3.7.1.2 Leaf area

In Experiments 1 and 4 the area of individual leaves at each position on the main stem was measured at full leaf expansion. In Experiment 1 all fully expanded leaves from five contiguous plants were removed on 7 December, 30 December, and 14 February. In Experiment 3 all fully expanded leaves were removed from three contiguous plants on 30 December, 25 January and 26 February. Leaf 1 was defined as the first leaf to emerge; leaves were then numbered acropetally until the leaf immediately below the tassel. The area of each individual leaf was determined using a Licor 3100 area meter (Licor Inc, Lincoln, NE, USA.)

3.7.1.3 Leaf senescence

Leaf senescence was also quantified in Experiments 1 and 4. The number of senesced leaves per plant was counted on the five marked plants used for leaf appearance measurements. A leaf was considered as being senesced when more than 50% of its fully expanded area had visibly yellowed. These measurements were recorded at the same time as the appearance of individual leaves until silking. Following this, measurements were taken at approximately 5-6 day intervals. The number of the highest senesced leaf was recorded on each plant.

Plate 2 'Challenger' sweet corn seedling indicating the nomenclature for defining fully expanded leaves. This plant has three fully expanded leaves and these are indicated by the arrows.

3.7.1.4 Primordia initiation

The initiation of leaf primordia was measured in Experiment 3. Two seedlings per plot were sampled from each replicate of the 0, 110, and 240 kg P ha^{-1} treatments on five dates at 5-9 day intervals beginning 3 days after emergence. Seedlings were examined under a binocular microscope. Individual leaf blades were removed systematically (and counted) until the last leaf primordium was visible on the apex. On these same seedlings the number of visible leaf tips and the date of tassel initiation were also recorded.

3.7.2 Radiation interception

3.7.2.1 Canopy analyser

GLAI was determined in Experiments 1 and 4 using a LAI-2000 canopy analyser (Licor Inc., Lincoln, NE, USA). Readings were taken in predominantly diffuse conditions (completely cloudy days or at dusk). In Experiment 1 seven measurements were taken (30 December 2001, 15 January, 22 January, 30 January, 12 February, 19 February and 10 March 2002) and in Experiment 3 five measurements were taken (7 January, 13 January, 22 January, 31 January and 1 March 2003). A sampling regime was used where one reading was taken above the canopy and four below. This was repeated twice for each plot. A 45° lens cap was used and the two sets of four below canopy readings were stratified across a row to account for the effect of the inter row gap.

3.7.3 Crop biomass harvests

Intermediate crop biomass was measured on six occasions for Experiments 1 and 4. The dates of sampling were 9 December 2001, 2 January, 11 January, 23 January, 7 February, and 21 February 2002 in Experiment 1. In Experiment 3 measurements were taken on 3 January, 12

January, 23 January, 31 January, 20 February and 6 March 2003. In Experiment 1 five contiguous plants were taken per sample, and in Experiment 3 three contiguous plants were sampled per plot.

These samples were then placed in a fan forced oven at 65 °C for at least 96 hours. Stem samples were divided into sections less than 50 mm in length to aid drying. These samples were then weighed using a Mettler Toledo PB1502 fine balance (Global Science and Technology Ltd, Glenfield, Auckland, NZ). These dry matter measurements were used to estimate crop biomass using the populations outlined in Appendix 3.

3.7.4 Crop phenology

3.7.4.1 Date of emergence

The mean date of emergence was measured in all experiments. In Experiment 1 only the 0, 100 and 200 kg P ha^{-1} plots were monitored. In Experiment 3 all crops were monitored. In each plot that was monitored, two 1 m length of row were marked with fibreglass stakes. During the period of emergence daily counts of the number of seedlings were taken for each plot until no further seedlings emerged. The date when 50% of the final number of emerged seedlings was determined retrospectively.

3.7.4.2 Silking

In each experiment, 20 contiguous plants were marked and monitored daily (over the silking period) to estimate the date of 50% silking. A plant was considered to have silked when silks were visible on the primary or uppermost ear, which was always the most developed.

3.7.4.3 Maturity

Harvest maturity (72% kernel moisture) was determined in all experiments. Three ears were randomly selected from each plot daily beginning approximately 20 days after silking. These ears were husked and the kernels stripped from them using a knife. A sub sample (70-200g) of

fresh kernel was weighed using a fine balance and then rapidly dried overnight at 105 (±5) °C for 12 hours. Preliminary data indicated a mean water loss rate of ~0.6% per day during this period. This value was used to predict maturity one day in advance, to schedule the final harvest.

3.7.5 Crop final harvests

3.7.5.1 Yield

Mature yield was determined from samples of 20 (2001/02) and 10 (2002/03) plants collected from the central row of each plot. Primary and secondary ears were removed and processed separately. The harvested plants were then cut at ground level and weighed fresh (Mettler Toledo, Spider 2) and a three-plant sub sample was taken to determine dry matter content. This sub sample was divided into stem and leaf fractions and then dried in a fan forced oven.

The total number of harvestable ears was recorded for each plot. An ear was defined as harvestable if it had at least 150 mm of filled cob length and was fully fertilised. The husk leaves were stripped from the cobs and weighed fresh (Mettler PC16 balance) and a 300 g sub sample of primary husk leaf was taken and dried in a fan forced oven.

The kernels were then cut from each of the original primary and the secondary ears using a knife. The fresh mass of the primary and secondary kernel fraction was determined. A 300 g sub sample of primary kernel was taken for dry matter determination and the mass of the primary and secondary rachis fractions was determined individually. A 300 g sub sample of rachis was taken for dry matter determination.

These data were used to reconstruct the components of yield for each treatment. To do this the mean plant population measured in Appendix 3 was used. The dry matter sub samples taken from the primary ear components were used to calculate both primary and secondary dry matter components. These are likely to differ as the primary ears are more developmentally advanced. However, the primary ears make up the major part of yield and therefore the error induced by this is likely to be small.

From these measurements the following components were calculated:

- Total crop dry matter (DM) (t ha^{-1})
- Vegetative ear DM (t ha^{-1}) (rachis and husk leaf, not including kernels)
- Kernel DM (t ha^{-1})
- Harvestable ears m^{-2}
- The percentage of kernel yield coming from primary ears
- Kernel recovery (Kernel DM as a proportion of the sum of vegetative ear DM and kernel DM)

3.7.5.2 Total P uptake

P uptake and its distribution at the time of final harvest were determined in Experiments 1 and 4 for two of the three replicates in each experiment. The samples of rachis, kernels, husk leaves, leaves and stems were ground to 0.5 microns using a Cyclotec 1093 sample mill (Foss, Sweden) and their P% determined using a nitric/perchloric acid digestion. The DM proportions of each component and its P concentration were then used to calculate the amount (kg ha^{-1}) of P in each component and the total in above ground biomass.

3.7.5.3 Yield components and ear dimensions

The number of kernel rows ear^{-1} and the number of kernels row^{-1} was counted on a five plant sub sample (primary ears) taken from the primary ears. These components were used to

calculate the mean number of kernels ear^{-1} by multiplying these two and the mean kernel mass (mg) using the kernel DM yield of primary ears.

The length (including unfilled portion) of individual ears from a 10 ear subsample (primary ears) was also determined. From this same sub sample the diameter (at the widest point) and the unfilled tip lengths were measured using a pair of callipers.

3.7.6 Environmental data

Air temperature, rainfall, and incoming solar radiation were taken from Broadfields' meteorological station. In addition, soil temperature and a second set of solar radiation data were collected at the site.

3.7.6.1 Soil temperatures

Soil temperatures were measured in Experiments 1 and 4 using a Hobo 4 channel external logger with TMC*x*-HA wide range temperature sensors (Onset Computer Corporation, Bourne, MA, USA). In Experiment 1 a single probe placed in a 200 kg P ha^{-1} plot was buried to a depth of 50 mm at sowing. In Experiment 3 probes were placed in a single P240 plot at sowing and these were monitored until 21 February. In each experiment the temperature sensor was placed within a row to more accurately reflect the temperature sensed by the plants than the inter-row soil. Temperature was recorded at hourly intervals.

3.7.6.2 Radiation

Measurements of solar radiation and photosynthetic photon flux density (PPFD) were taken from Experiments 1 and 4. All measurements were taken at 5-minute intervals and averaged for each hour. They were recorded using a Datataker DT-600 data logger (Datataker, Rowville, VIC, Australia). All measurements began within two weeks of crop emergence but

due to equipment failure a complete data set was not recorded in both experiments. The measurements were logged every hour taken from measurements every minute. The incoming solar radiation measured at the site (incomplete) was regressed against daily solar radiation measurements at Broadfields' meteorological station (Appendix 5). There was close agreement between the two data sets. Therefore, in subsequent analyses requiring incoming solar radiation the complete data set from Broadfields' meteorological station was used. The data measured at the site were used for the calculation of the proportion of radiation intercepted in Section 5.2.4.

Above-canopy measurements of total solar radiation (W m^{-2}) were measured using a Licor Pyranometer LI 200SA at a central point of the experiment. Below-canopy measurements were taken in Experiment 3, using a single sensor placed across a row in each of the P240 and P0 plots. Tube solarimeters were positioned in the appropriate plot on 7 December 2002 and measurements were taken until 8 April 2003. Due to the solarimeters being 330 mm and the row spacing being 700 mm (Section 3.5.1) these tube solarimeters were moved periodically (approximately 10-12 days) between positions that were within the row and between the row to take account of spatial differences in radiation interception.

3.8 Statistical analyses

All relevant statistical procedures are outlined in the appropriate results chapters. All ANOVA procedures have used a randomised complete block design structure with means separation based on Fisher's protected least significant difference ($p<0.05$). All statistical analysis used Genstat 5, release 4.2 (Lawes Agricultural Trust, Rothamsted experimental station, UK, 2001). Where regressions have been fitted to data, individual curves have been fitted to each plot (unless otherwise stated) and then individual curve coefficients tested using ANOVA.

Chapter 4. Yield, quality, and partitioning of 'Challenger' sweet corn in response to fertiliser N and P.

4.1 Introduction

This chapter focuses on the agronomic responses of 'Challenger' sweet corn (Experiments 1, 4 and 5) to applied P fertiliser, with responses to N fertiliser (Experiment 2) included for comparison. In sweet corn the economic component of yield is determined by the crop end use. Therefore the partitioning of crop DM into vegetative parts, ears and kernels is included as part of the crop HI (Section 2.3.4). Sweet corn value is also determined by ear quality (Section 2.4). Therefore the relationships between ear dimensions or yield structure and crop DM yield are examined across data sets from Experiments 1, 2, 4 and 5.

Understanding crop development is important for scheduling and quantifying the risks of sweet corn production (Section 2.5). The effects of P fertiliser (Experiments 1 and 4) on crop development are therefore examined by quantifying Tt requirements to emergence, silking, and canning maturity for 'Challenger' sweet corn.

4.2 Materials and methods

The methods used to measure the agronomic yield data used in this chapter were outlined in Section 3.7.5. Data are taken from Experiments 1, 2, 4 and 5 (Sections 3.3 and 3.4).

4.2.1 Soil fertility

The Olsen P prior to the commencement of the experiments was 6 μg ml^{-1} (Table 3.1). Olsen P data for comparison of the P fertiliser rates were collected following the completion of each field experiment and are included in Appendix 2. In addition mineralisable soil N in an

adjacent field experiment ~50 m from the site averaged 61 kg N ha^{-1} and ranged from 43 to 106 kg N ha^{-1} (D.R. Wilson *pers. comm.*).

4.2.2 Calculations and analysis

4.2.2.1 Nutrient response curves

Total crop DM and kernel DM (Section 3.7.5.1) were measured from 20 plants per plot in the four fertiliser response experiments (1, 2, 4 and 5). Results were tested using ANOVA (Section 3.8) with both linear and quadratic contrasts. These data were also tested with a non-linear regression analysis using an asymptotic function (Equation 4.1). The appropriate response function was selected based on the highest F probability value for each data set.

$$Y = A - B \times R^x$$

Equation 4.1

Where A is the asymptote (or maximum yield) (t ha^{-1}); B is the reduction from the maximum yield when no fertiliser was applied (t ha^{-1}); and R determines the curvature of the response.

In 2001/02 Experiments 1 and 2 were analysed separately, while in 2002/03 the non-linear regression analysis was fitted to the combined data from both Experiments 3 and 4. This gave a range of total applied P over the two years from 0 to 380 kg ha^{-1} for this regression. The decision to combine these data sets was based on paired t-tests for total crop DM and total kernel DM, which indicated that the 240 kg P ha^{-1} treatments common to both Experiments 3 and 4 were not different ($p<0.05$).

Experiment 3 (2002/03) used the same experimental plots to repeat Experiment 1 (2001/02). As a consequence the results of the two experiments were confounded and it was not possible to statistically test differences in P responses between seasons.

4.2.2.2 Relationships between biomass components

The relationships between total crop DM and kernel DM, vegetative DM, ear DM (excluding kernels) (Section 3.7.5.1) were examined using least squares regression set to pass through the origin. This was based on the fact that when total crop biomass is 0 t DM ha^{-1} the component parts must also be 0 t DM ha^{-1}. Therefore the slope of each regression represents the mean proportion of total crop DM partitioned to each crop component. The results of the unconstrained regressions are supplied in Appendix 6.

Relationships between total crop DM and the number of harvestable ears, the proportion of total kernel yield coming from primary ears, and kernel recovery (Section 3.7.5.1) were also examined using least squares regression for the data from Experiments 1, 2, 4 and 5.

4.2.2.3 Yield structure and ear dimensions

Kernels ear^{-1}, rows ear^{-1}, kernels row^{-1} (Section 3.7.5.2) and mass of individual kernels from primary ears were examined using least squares regression against total kernel DM per individual primary ear for the combined data sets. The mass of individual kernels was calculated from the mean number of kernels per ear and the kernel DM per ear for each plot and did not include unfilled kernels. Kernel DM yield per primary ear was used as an indicator of assimilate supply. The aim was to examine how varying assimilate supply, caused by the fertiliser treatments, affected the individual components of yield. Ear dimensions of length, diameter, and unfilled tip length (Section 3.7.5.2) were also related to kernel DM yield

per primary ear using least squares regression. These variables were only examined for primary ears on the basis that these ears provide the bulk of harvestable ears used for fresh market sales.

4.2.2.4 Crop development response to P

Dates of 50% crop emergence (Section 3.7.4.1), 50% silking (Section 3.7.4.2) and crop canning maturity (72% kernel moisture) (Section 3.7.4.3) for the responses to P fertiliser (Experiments 1 and 4) were used in these analyses. The dates of 50% crop emergence and 50% silking were discrete variables taken from daily observations and therefore were accurate measures of development. However, canning maturity was estimated by determining the kernel moisture % on a three-ear sub sample taken daily (Section 3.7.4.3). Due to the subjectivity in estimating canning maturity and the fact that this stage was estimated one day in advance the dates when harvest actually occurred were not considered reliable for studying development. Kernel moisture % from the final harvest (Appendix 7) indicated an inconsistent prediction of canning maturity. Thus actual crop maturity data were corrected assuming a 0.6% loss in kernel moisture per day (Brooking, 1990; Brooking and McPherson, 1989). These corrected canning maturity dates were then used in all subsequent analyses.

The durations of the three pheno-phases between sowing and emergence, emergence and silking, and silking and maturity were calculated using both calendar days and Tt (Equation 2.5). Thermal time was calculated using a modified sine curve to calculate Tt for eight separate three-hour intervals per day and these were integrated for each day (Jones and Kiniry, 1986) (Section 2.5.1). Thermal time was calculated using 50 mm (the approximate sowing depth) soil temperature measured at the experimental site (Section 3.7.6.1) and T_b of 8°C for the sowing to emergence phase. Air temperature measured at Broadfields'

meteorological station (Section 3.2.4) was used to calculate Tt for emergence to silking and silking to maturity, using T_b of 8 °C and 0 °C, respectively (Appendix 8, Section 2.5.1).

The relationship between temperature and Tt was linear between T_b and T_{opt} as temperature never exceeded 34 °C (Section 2.5.1). Any effect of photoperiod on development was ignored on the basis that it would be minor for sweet corn (Brooking and McPherson, 1989; Olsen *et al.*, 1993).

The relationships between the duration (in Tt using appropriate T_b's) of the emergence to silking and silking to maturity phenophases were examined using least squares regression. Mean data from each treatment were used from Experiments 1 and 4 (2001/02 and 2002/03).

4.3 Results

4.3.1 Biomass and kernel response curves

Total crop DM did not respond to fertiliser N and averaged 12.9 t ha^{-1} (Figure 4.1a). However, there was a quadratic response of kernel DM yield to fertiliser N, with ~ 2.7 t DM ha^{-1} of kernels when no N was applied and increasing to a maximum of 3.6 t ha^{-1} with ~ 170 kg N ha^{-1} (Figure 4.1b).

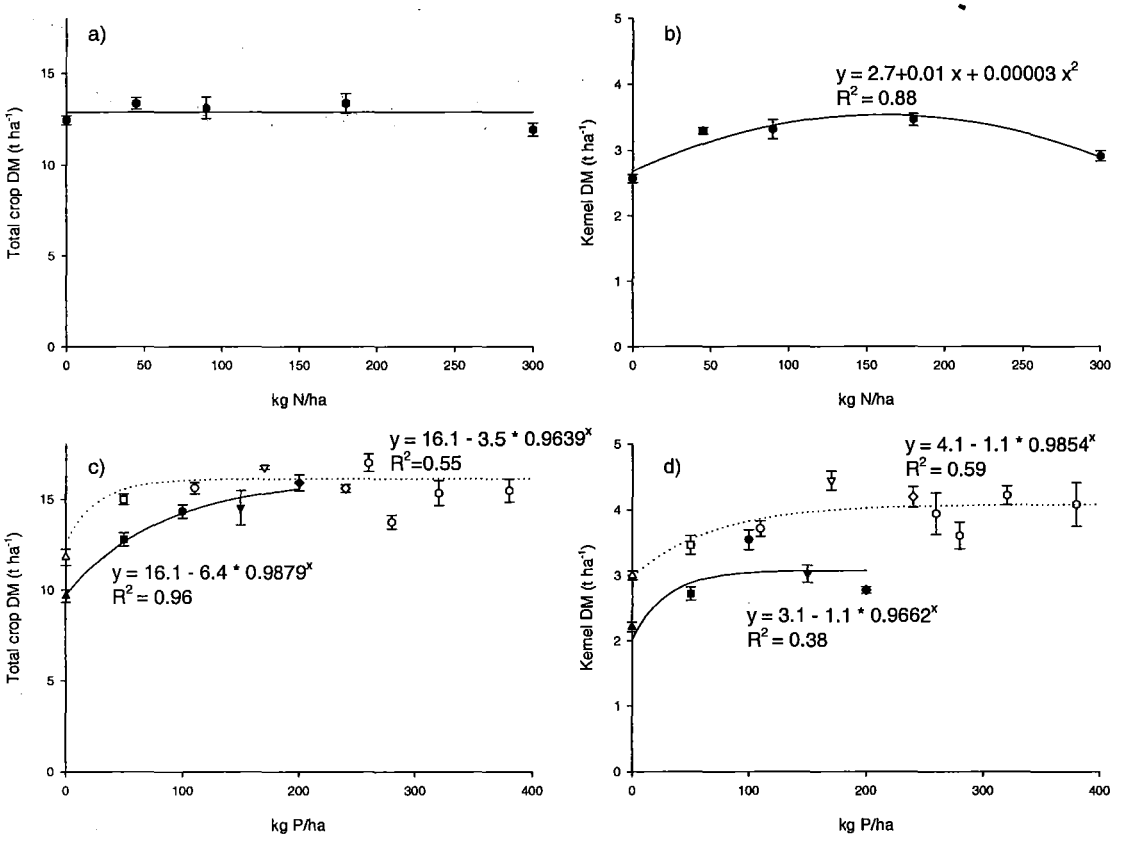

Figure 4.1 Total crop DM (a and c) and total kernel DM (b and d) yield responses of 'Challenger' sweet corn to N (a and b) and P (c and d) fertiliser at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03. Symbols represent treatments outlined in Table 4.1. Error bars represent 1 standard error of the mean.

Table 4.1 Symbols and the treatments they represent in all figures presented in this thesis.

2001/02			2002/03		
Symbol	Treatment (kg P/ha)	Experiment	Symbol	Treatment (kg P/ha)	Experiment
▲	0	1	△	0	3
■	50	1	□	50	3
●	100	1	○	110	3
▼	150	1	▽	170	3
◆	200	1	◇	240	3 and 4
●	0-300 kg N/ha	2	○	260-380	4

There was an asymptotic (R^2=0.96 and 0.55) increase ($p<0.01$) in total crop DM with increasing fertiliser P in both 2001/02 and 2002/03 (Figure 4.1c). In 2001/02, 95% of the asymptotic yield would have been achieved with 250 kg P ha^{-1}, with a mean response of 25 kg DM kg^{-1} P in the range from 0 to 250 kg P ha^{-1}. In 2002/03, 95% of maximum yield was achieved with 80 kg P ha^{-1}, with a mean linear response of 41 kg DM kg^{-1} P in the range between 0 and 80 kg P ha^{-1} (Figure 4.1c).

There was also a trend for total kernel DM to increase ($p<0.05$) asymptotically (R^2=0.38 and 0.59) with P fertiliser in both seasons (Figure 4.1d). The asymptotes for kernel yield (**A**) were 3.1 (±0.29) t ha^{-1} in 2001/02 and 4.1 (±0.15) t ha^{-1} in 2002/03. In both seasons there was ~ 1.1 t ha^{-1} less kernel mass when no P fertiliser was supplied.

4.3.2 Biomass partitioning

Linear regressions of the individual biomass components against total crop DM showed that 44% was vegetative parts (i.e. leaves and stem) (Figure 4.2a), 32% was ears (excluding

kernels) (Figure 4.2b), and 24% was kernels (Figure 4.2c) irrespective of crop DM or fertiliser treatment.

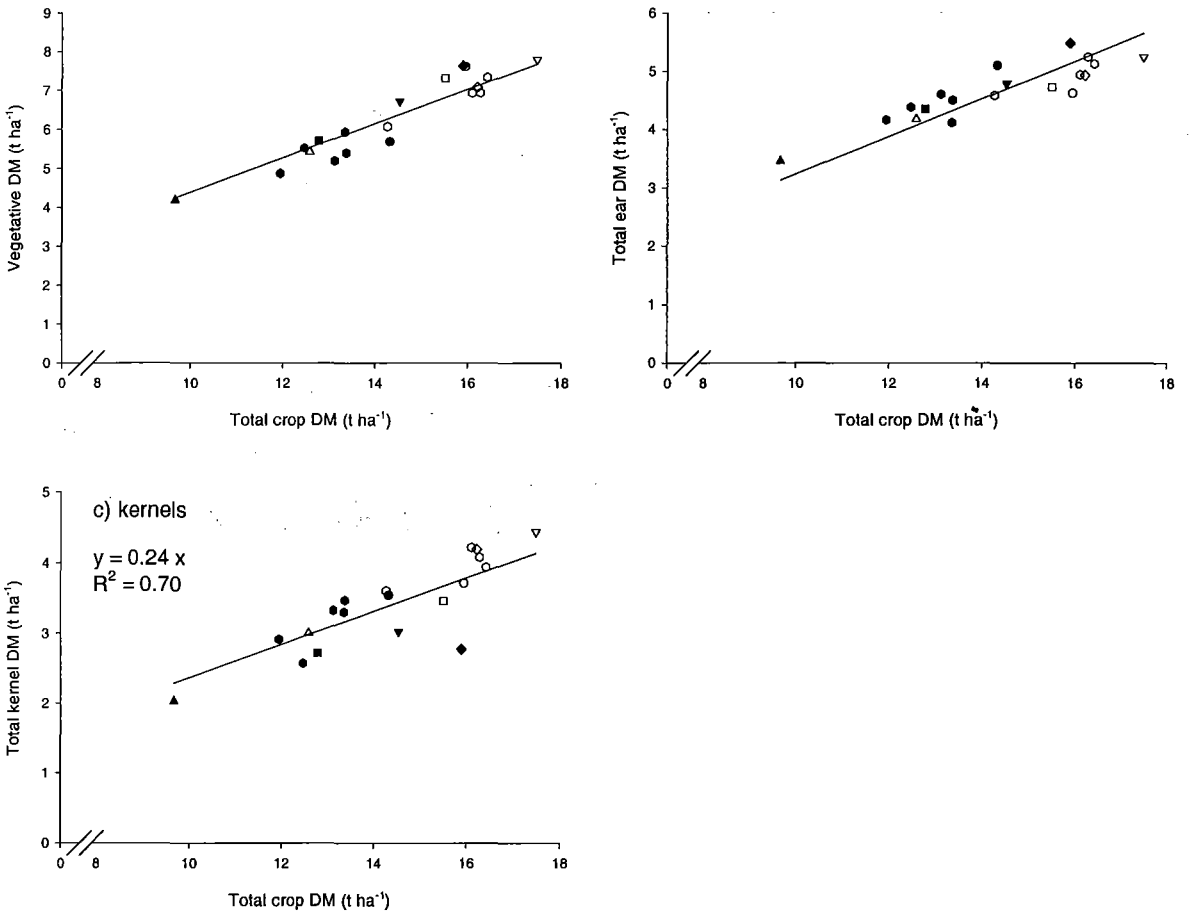

Figure 4.2 Components of total crop dry matter against total crop DM for combined data sets of 'Challenger' sweet corn (Experiments 1,2,4 and 5), grown at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03 (Symbols in Table 4.1). The components are vegetative plant parts (a) (t ha^{-1}), ears (b) (t ha^{-1}) and kernels (c) (t ha^{-1}) .

Additionally the strong linear relationship (Figure 4.3a), indicated that the number of harvestable ears m^{-2} increased by 0.36 (±0.06) for every 1 t ha^{-1} increase in total crop DM (R^2=0.70). There were also weak linear relationships between the proportion of kernel

biomass coming from primary ears (R^2=0.26), and kernel recovery (R^2= 0.19 (Figure 4.3b and c) against total crop DM. These indicated a 1.3(±0.5)% decrease in the proportion of kernel yield contributed from primary ears (Figure 4.3 b) and a 0.85% (±0.37) increase in kernel recovery (Figure 4.3 c) for each additional 1 t ha^{-1} of total crop DM.

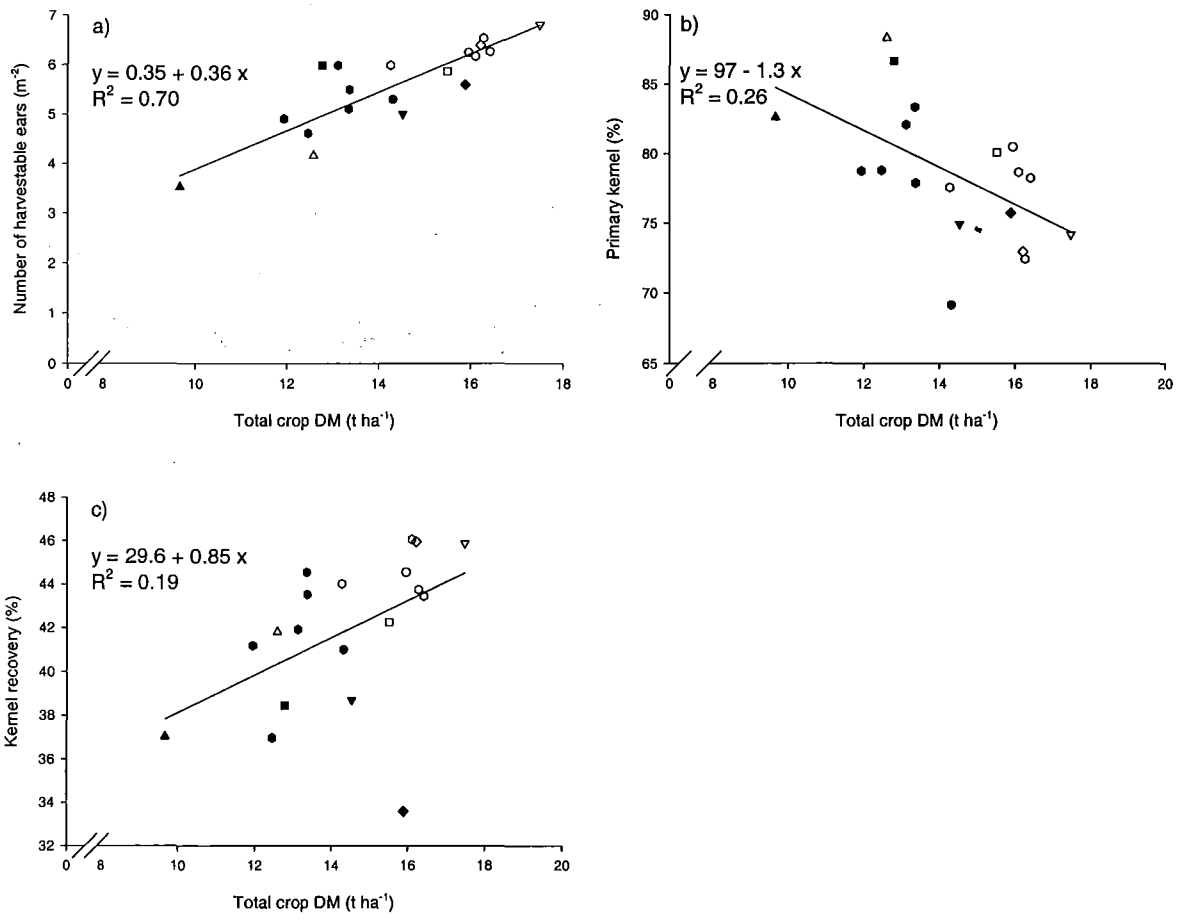

Figure 4.3 Number of harvestable ears m^{-2} (a), percentage of total kernel DM coming from primary ears (b), and kernel recovery % (c) against total crop DM for combined data sets (Experiments 1, 2, 4, and 5) of 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03 (Symbols in Table 4.1).

4.3.3 Yield structure and ear dimensions

There was no relationship between total kernel DM per primary ear and either the number of kernels ear^{-1} or the number of rows ear^{-1} (Figure 4.4a and b). However, the 0 kg P ha^{-1} treatment in 2001/02 was an outlier in both relationships with 490 kernels ear^{-1} ($p<0.05$) compared with 570 kernels ear^{-1} for all other treatments and 15.2 rows ear^{-1} compared with 16.9 rows ear^{-1} in all other treatments.

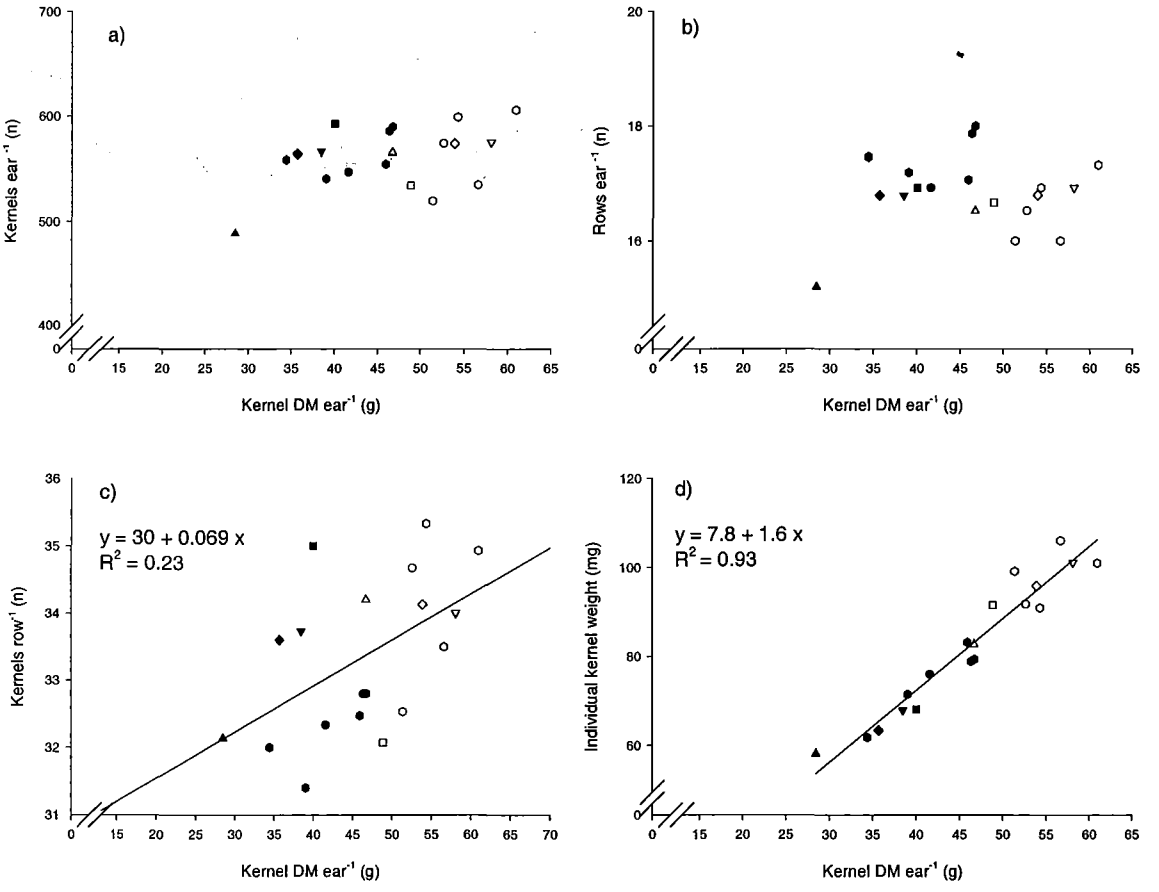

Figure 4.4 Number of kernels ear^{-1} (a), rows ear^{-1} (b), kernels row^{-1} (c), and the individual kernel mass (d) against kernel DM per primary ear for combined data sets (Experiments 1, 2, 4, and 5) of 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03 (Symbols in Table 4.1).

The weak (R^2=23%) linear increase in the number of kernels row^{-1} (Figure 4.4c) contrasts the 1.6 mg increase (R^2 = 0.93) in mean individual kernel mass for every 1 g increase in total kernel DM of primary ears (Figure 4.4d).

Mean ear diameter increased (R^2=0.74) by 0.1 mm (Figure 4.5a) for every 1 g increase in total kernel DM of the primary ears, but the overall range was only 5 mm. Mean ear length was not related to total kernel DM per primary ear (Figure 4.5b).

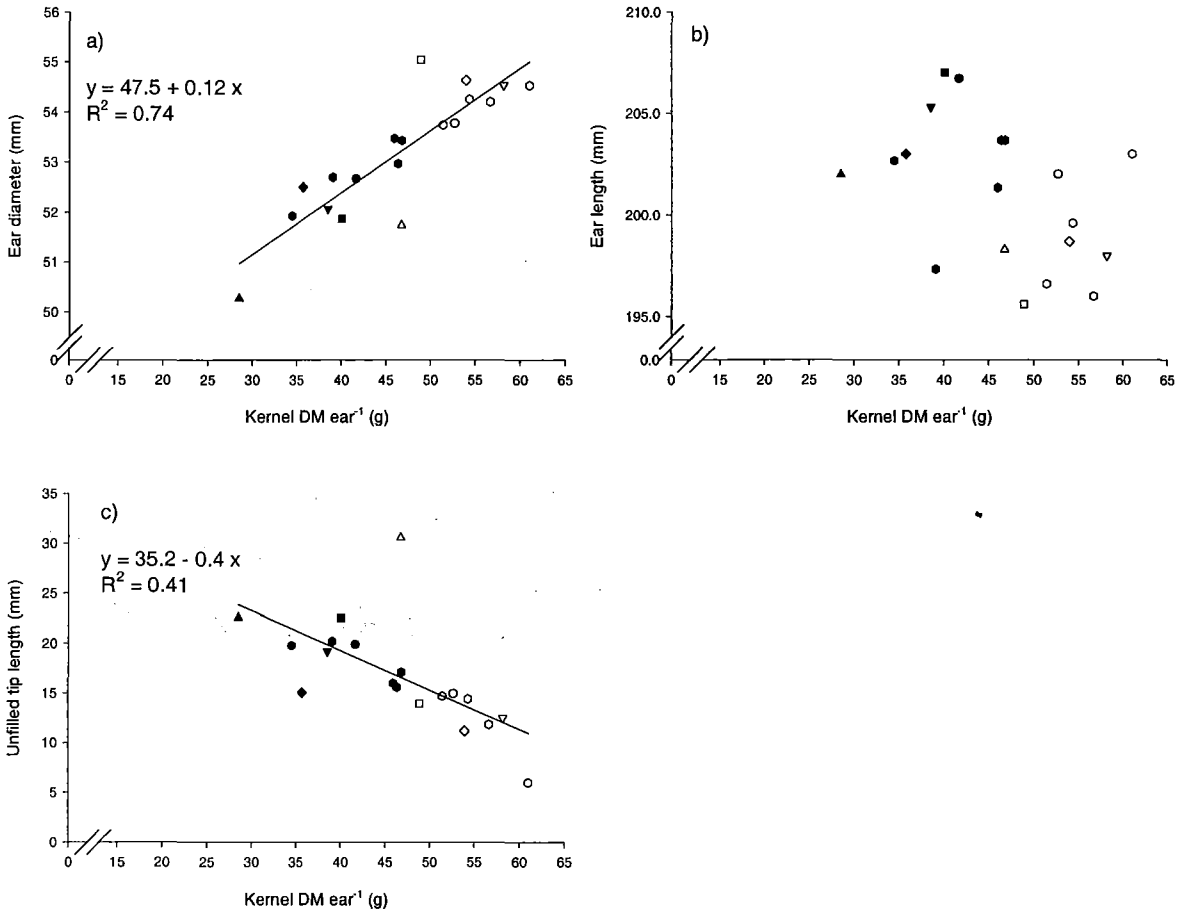

Figure 4.5 Mean ear diameter (mm) (a), mean ear length (mm) (b), and unfilled tip length (mm) (c), against kernel DM (g) per primary ear for combined data sets (Experiments 1, 2, 4, and 5) of 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03. (Symbols in Table 4.1).

Unfilled tip length decreased by 0.4 mm for every 1 g increase in kernel DM per primary ear (Figure 4.5c). In both seasons crops receiving no P fertiliser had the highest mean unfilled tip length because they had the least kernel DM yield per primary ear.

4.3.4 Crop development in response to P fertiliser

4.3.4.1 Sowing to emergence

Emergence was uniform from all P treatments in both seasons. The time of 50% crop emergence occurred 14 days or 115 °Cd (T_b = 8 °C) after sowing in 2001/02 and 16 days or 120 °Cd after sowing in 2002/03.

4.3.4.2 Duration of emergence to maturity, emergence to silking, and silking to maturity periods.

In 2001/02 crops receiving 0 kg P ha^{-1} reached canning maturity after 149 days which was 7 days longer ($p<0.01$) than the 200 kg P ha^{-1} treatments. In 2002/03 canning maturity occurred 136 days after emergence for 0 kg P ha^{-1} crop and after 130 days for 240 kg P ha^{-1} crops (Table 4.2).

The differences in total crop duration were caused mainly by changes in the period from emergence to silking. In 2001/02 this decreased by 15 days from 97 days (725 °Cd; T_b = 8°C) with no P fertiliser, to 82 days (610 °Cd) with 200 kg P ha^{-1}. In 2002/03 it decreased ($p<0.01$) from 81 days (645 °Cd) with no P fertiliser to 72 days (565 °Cd) with 240 kg P ha^{-1} (Table 4.2).

In 2001/02 there was an increase ($p<0.01$) in the duration of the silking to maturity phase from 52 days (762°Cd) with no P fertiliser to 59 days (910 °Cd) with 200 kg P ha^{-1}. In contrast there was no change in the number of days between silking and maturity (56 days) in 2002/03. When this duration was evaluated in Tt (T_b = 0°C), it increased ($p<0.1$) from 810 °Cd to 900 °Cd between the 0 and 240kg P ha^{-1} crops (Table 4.2).

Table 4.2 Time (days and °Cd) for phenological development of 'Challenger' sweet corn, at five rates of P fertiliser when grown at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03. Results are for three phases: emergence-maturity (emerg-mat), emergence-silking (emerg-silk), and silking –maturity (silk-mat).

kg P ha^{-1}	Emerg-Mat (days)	Emerg-Silk (days)	Silk-Mat (days)	Emerg-Silk (°Cd T_b=8°C)	Silk–Mat (°Cd T_b=0 °C)
2001/02 (Experiment 1)					
0	149	97	52	725	760
50	146	89	57	665	855
100	144	88	55	660	840
150	141	84	57	625	870
200	142	82	59	610	905
α	<0.05	<0.001	<0.001	0.001	<0.001
s.e.	1.5	1.5	0.7	12	11
2002/03 (Experiment 3)					
0	136	81	54	645	810
50	132	76	56	590	865
110	129	74	56	575	875
170	130	73	57	570	885
240	130	72	58	565	900
α	<0.01	0.01	n.s.	<0.01	<0.1
s.e.	0.9	1.4	1.2	10	19

α = F probability, **n.s.** =not significant, **s.e.**= pooled standard error of the mean.

4.3.4.3 Relationship between emergence to silking and silking to maturity periods.

There was a strong (R^2 = 0.68) negative linear relationship between Tt for emergence-silking and silking–maturity (Figure 4.6). For every 1 °Cd increase in Tt (T_b = 8 °C) between emergence and silking, there was a 0.7 °Cd decrease in the Tt (T_b = 0°C) between silking and maturity. Confidence intervals (95%) of separate regressions for each season overlapped so a single regression was calculated.

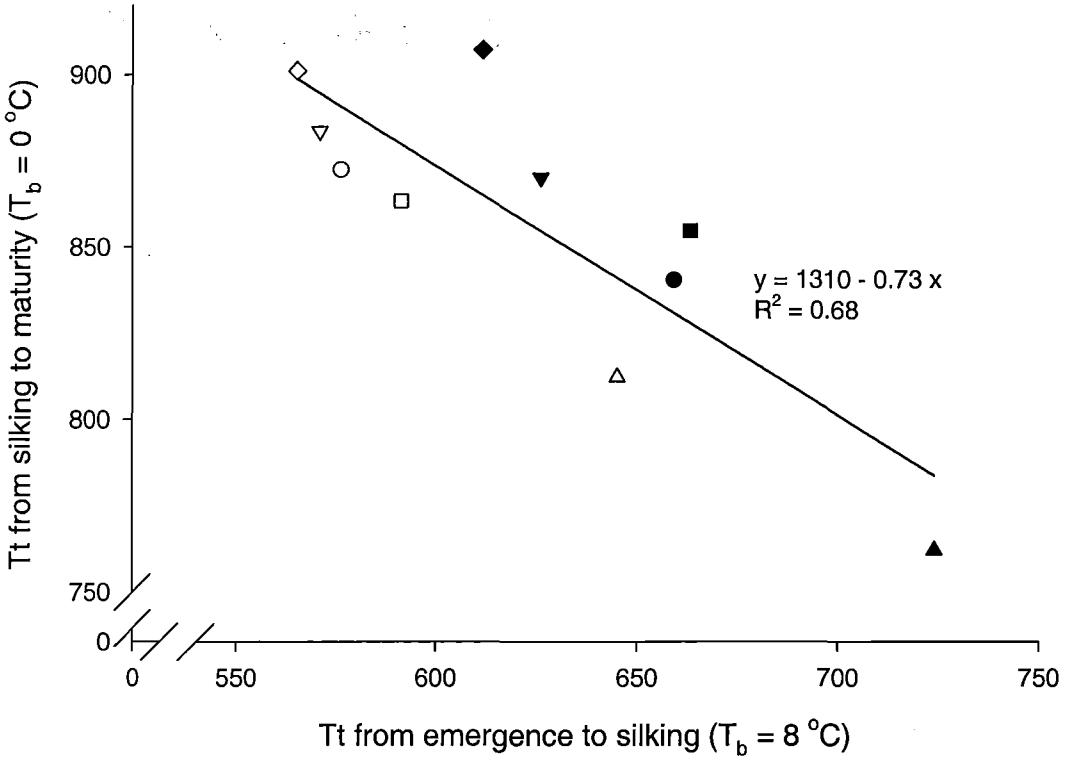

Figure 4.6 Relationship between Tt from silking to maturity against Tt for emergence to silking for 'Challenger' sweet corn grown at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03. (Symbols in Table 4.1).

4.4 Discussion

4.4.1 Total crop DM and kernel DM yield

4.4.1.1 Nitrogen

Previous literature indicates that fertiliser N may increase sweet corn yield (Section 2.2.1) but N fertiliser did not increase total crop DM (Figure 4.1a) and had only a minor quadratic effect on kernel yield (Figure 4.1b) in Experiment 2. This was most likely because soil N was generally sufficient for maximum 'Challenger' sweet corn yield. In an adjacent field experiment mineralisable N averaged 61 kg N ha^{-1} to 150 mm depth but varied from 43 to 106 kg N ha^{-1} (D.R. Wilson *pers. comm.*). However, a 12.9 t ha^{-1} sweet corn crop (Figure 4.1a) consisting of ~1.3% N (Jones, 1983) would contain 165 kg N ha^{-1}. Sweet corn crops in Experiment 2 were probably accessing N reserves below 150 mm which had accumulated over the previous 15 years of clover based pasture. The response to fertiliser N (Experiment 2) is not considered further in this thesis.

4.4.1.2 Phosphorus

The asymptotic increases in both total crop DM and kernel DM yield with P fertiliser (Figure 4.1c and d) were expected because of the low (6 μg ml^{-1}) initial soil P levels compared with the recommendations of 30-35 μg P ml^{-1} (Clarke *et al.*, 1986) for sweet corn in New Zealand. This asymptotic P response is site and season specific (Section 2.2.2) and ignores the role of the environment in determining potential yields (Reid, 2002). The response is due to each incremental increase in P fertiliser acting against a smaller deficiency. In the current experiments the asymptote was ~16 t crop DM ha^{-1} in both seasons (Figure 4.1c).

These sweet corn crops had a total seasonal P uptake of between 15 and 33 kg P ha^{-1}, depending on P fertiliser treatment (Appendix 9). The 0 kg P ha^{-1} treatments had the lowest

uptake of P of 15 and 23 kg P ha^{-1} in Experiments 1 and 4 respectively. When P fertiliser was applied the values of total P uptake were between 24-33 kg P ha^{-1}. This is consistent with the uptake of P in maize crops of 24-34 kg P ha^{-1} (Hanway, 1962). In the study of Hanway (1962) 70-80% of total P uptake was in the grain. In the current experiments this was much less (~40-50%), possibly due to sweet corn being harvested before physiological maturity. The total uptake of P was small (~5%) compared with that applied (Appendix 9). However, this low utilisation of fertiliser P is consistent with other research where frequently >20% of the P applied is taken up in the first crop (Vance *et al.*, 2003).

In Experiment 1 the 0 kg P ha^{-1} crops took up substantially less than the same treatment in Experiment 3. This is likely to be associated with the onset of late water stress (Figure 3.2) in Experiment 1. This late water stress may have limited the uptake of soil P. This is confirmed by looking at the distribution of P within the plant (Appendix 9). In Experiment 1 the uptake of P in the vegetative structures (leaves and stems) is comparative between the two seasons. In contrast, there is substantially more P in the reproductive structure (husk leaves, kernels and rachis) of the 0 kg P ha^{-1} crops in Experiment 3 compared with Experiment 1. The uptake of soil P post silking in Experiment 1 may have been limited by an insufficient water supply.

4.4.2 Biomass partitioning

The asymptotic responses of kernel DM yield to P (Figure 4.1d), were due to the asymptotic responses of total crop DM (Figure 4.1c). In these same crops the partitioning of yield into biomass components was conservative (Figure 4.2). This was consistent with the primary effect of nutrient stress being to reduce crop DM and a secondary effect of reducing crop HI in maize (Figure 2.6). The proportion of crop DM partitioned to kernels was 24% (Figure 4.2c). This is consistent with other examples in 'Challenger' sweet corn (Figure 2.5).

4.4.3 Economic yield relationships

For a processor, FM yield of kernels is of primary importance and kernel DM can be easily converted to kernel FM by assuming that kernel moisture was 72%. As total crop DM increased the kernel recovery increased (Figure 4.3 c). The advantages to the processor, of applying P would come from greater yields and more efficient processing through increased kernel recovery.

For fresh market sales, the number of harvestable ears is a primary determinant of economic value. This was strongly related to total crop DM (Figure 4.3 a), which can be attributed to the hierarchy of assimilate supply between primary and secondary ears. Generally secondary ears were a minor contributor to kernel DM yield (<30%), and few were regarded as harvestable (filled ear length >150 mm). For every 1 t ha^{-1} increase in crop DM the contribution of secondary ears increased by 1.3% (Figure 4.3 b) and their relative sizes would also have increased. Therefore the numbers of harvestable secondary ears increased and hence the total number of harvestable ears increased. This supports the hypothesis of Rogers *et al.* (2000) that primary ears are the principal recipients of assimilate.

4.4.4 Yield structure and ear dimensions

There was no affect of assimilate supply (kernel DM per ear) on the number of kernels row^{-1} or rows ear^{-1} (Figure 4.4a-c). These were probably under strong genetic control. Consequently, changes in kernel yield with P (Figure 4.1d) were closely associated with the mass of individual kernels (Figure 4.4d) which is determined post silking (Borras *et al.*, 2002).

Ear dimensions are pivotal parts of fresh market ear quality. Ear lengths (195-210 mm) were unaffected (Figure 4.5c) and ear diameter (50-55 mm) responses to P supply were only minor. Changes in ear diameter were economically unimportant but confirmed the effect of P on individual kernel mass. (Figure 4.4d). Fresh market consumers prefer an ear that is filled to the tip (Tracy, 2001), and therefore lack of P supply reduced sweet corn quality (Figure 4.5c). The decrease in unfilled tip length and the increase in ear diameter with increased total crop DM were consistent with the linear range between 100 and 350 g FM plant^{-1} (Figure 2.8).

4.4.5 Crop development

Crop emergence was uniform across P treatments and took ~120 °Cd (T_b = 8 °C). This was slower than maize (~95 °Cd) (Stone *et al.*, 1999) probably because sweet corn has reduced seed reserves to remobilise for seedling growth.

The 6-7 day delay in canning maturity when no P fertiliser was applied was mainly due to a delay in the onset of silking (Table 4.2). This delay may increase the already high risk of crop failure in Canterbury (Wilson and Salinger, 1994). This point is examined further in Section 7.3.3.2.

The effect of both P and N stress on crop phenology has been demonstrated previously (Section 2.5.2) and changes in phenology were most likely due to the impact on plant growth. For example in the 0 kg P ha^{-1} crops, physiologically silk development may have occurred but growth after initiation was restricted, and therefore their appearance was reduced. This point is illustrated by the negative relationship between the Tt for the emergence-silking and

silking-maturity phases (Figure 4.5). The differences in development between the P treatments in 2002/03 are illustrated in Plate 3, Plate 4 and Plate 5.

4.4.5.1 Seasonal differences in development

Silking occurred 47 °Cd (T_b = 8 C) earlier in 2002/03 compared with 2001/02. Development was related to Tt based on air temperature ~3 km East of the site (Section 3.2.4). Between seasons a row of trees adjacent to the site were removed. This may have led to an 'uncoupling' of the Broadfields temperature data with that at the experimental site, giving rise to the apparent discrepancy in development. A minor change (~+0.5°C) in mean air temperatures between the Broadfields meteorological station and the experimental site between the two seasons could account for this difference both in terms of days and Tt.

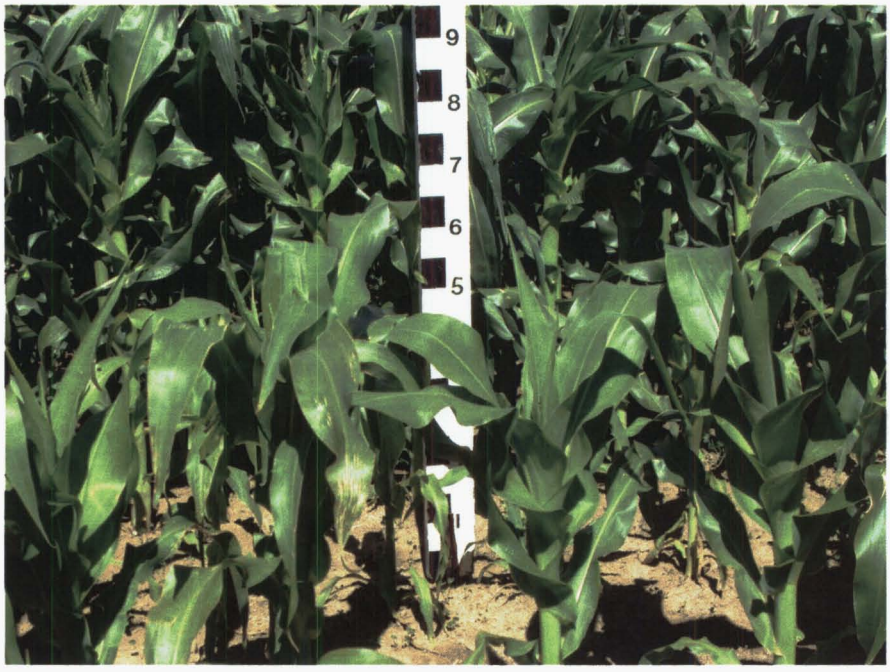

Plate 3 A 0 kg P ha^{-1} crop from Experiment 3 (2002/03) on 29 January 2003. As well as the poor growth, note the lack of visible tassels.

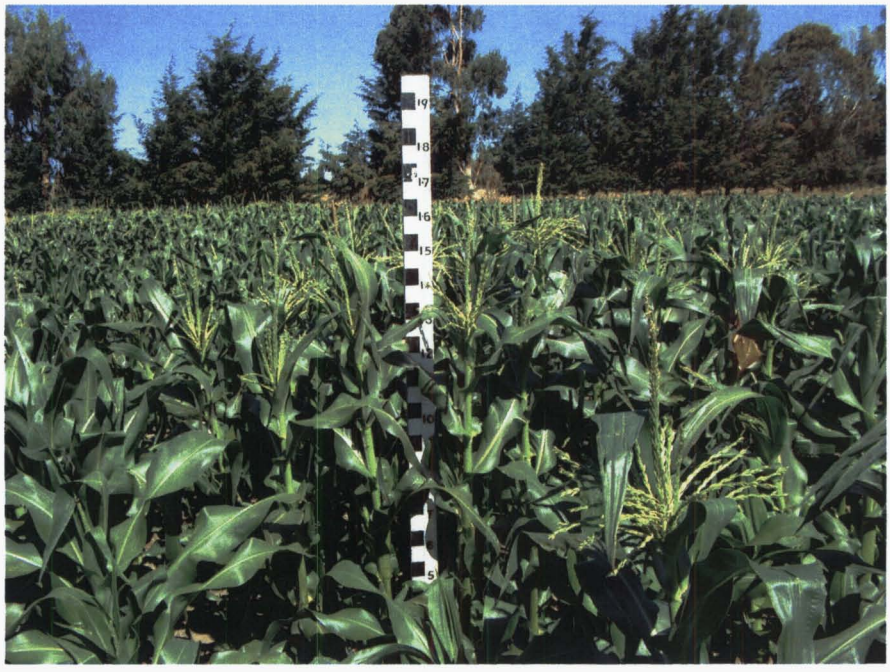

Plate 4 A 240 kg P ha^{-1} crop from Experiment 3 (2002/03) on 29 January 2003. Note the immature tassels that are clearly visible.

Plate 5 Ears from a 0 kg P ha^{-1} crop (left) and a 204 kg P ha^{-1} crop (right) in Experiment on 12 February 2003. Note that the 0 kg P ha^{-1} ear has no visible silks but that the 240 kg P ha^{-1} ear has many visible silks.

4.5 Conclusions

- N fertiliser did not increase total crop DM, whereas P fertiliser gave a marked increase in both total crop and kernel DM.
- Total crop DM was conservatively partitioned to vegetative parts (44%), ears (32%), and kernels (24%) regardless of N or P fertiliser treatment and the increased total crop DM gave an increased number of harvestable ears.
- Ear structure and dimensions were relatively stable. Kernel DM yield differences were strongly related to kernel filling (i.e. individual kernel mass, and unfilled tip length) rather than kernel number per ear.
- Crop maturity was delayed in crops receiving no P fertiliser, as a consequence of a delay in silking.

Based on these the role of P fertiliser in determining 'Challenger' sweet corn total crop DM yield will be explored further in this thesis on the basis that this is strongly related to all other measures of yield and quality. Chapter 5 investigates RI_{cum} and its component processes; and Chapter 6 addresses the effects of P supply on RUE.

Chapter 5. Fertiliser P effects on GLAI development and solar radiation interception in 'Challenger' sweet corn.

5.1 Introduction

In Chapter 4 the yield responses of 'Challenger' sweet corn crops to different forms and rates of fertiliser were described. There was only a minor response to N. Thus no further analysis of N response was conducted with emphasis on the differences in total crop DM yield in response to P. These differences may have resulted from the interception of more solar radiation or differences in the RUE (Equation 1.1). The first step in explaining the mechanisms behind crop yield differences is an accurate quantification of the amount of radiation intercepted by each crop.

To do this accumulated intercepted solar radiation (RI_{cum}) is calculated as the sum of daily RI for the duration of the crop from emergence to harvest. Differences in the amount of daily RI are dependent on the actual daily green LAI (GLAI) and the extinction coefficient (k) which may both differ among crops. In this chapter the components of total LAI (TLAI i.e. LAI including senesced leaves) are examined to determine the temporal pattern of TLAI development. Daily TLAI is then reconstructed (Section 2.3.1.4) and tested against discrete field data collected using the LAI-2000 canopy analyser (Section 3.7.2.1).

The reconstructed TLAI and observed leaf senescence data (Section 3.7.1.3) are then used to calculate the fraction of senesced leaf area (FSA) and examine the effects of P fertiliser on this. Finally, GLAI is calculated by subtracting FSA from TLAI. This method of estimating TLAI and GLAI has been used previously with sweet corn (Stone *et al.*, 2001b) and is similar to the method used in maize models (e.g. Muchow *et al.*, 1990). The value of k is calculated

from the relationship between RI_{frac}, calculated from solar radiation data logged from the 0 and 240 kg P ha^{-1} crops in Experiment 3, and TLAI. Reconstructed GLAI and k values are then used to calculate RI_{cum} for each crop.

5.2 Materials and methods

The materials and methods used to measure leaf appearance, the area of individual leaves and leaf senescence were described in Section 3.7.1 with additional details in Section 6.2.2.2. Data were collected at 3-4 day intervals from Experiments 1 and 4. The data used to quantify RI_{frac} were taken from single tube solarimeters placed at ground level in each of the 0 kg P ha^{-1} (2 replicates) and 240 kg P ha^{-1} (3 replicates) crops in Experiment 3 (2002/03) and a single central pyranometer ~2.5 m above the experimental area (Section 3.7.6.2).

The data used for calculating incoming solar radiation in the RI_{cum} analysis (Section 5.3.4.2) were measured daily at Broadfields' meteorological station ~ 3km east of the site (Section 3.7.6.2). These calculations were made with the daily solar radiation data at Broadfields' and not that measured at the site, due to the incomplete data set collected at the site, i.e. solar radiation was not logged throughout the entire duration of each of Experiments 1 and 4. There was a strong linear relationship between the incomplete above canopy solar radiation raw data measured with the pyranometer (Section 3.7.6.2) and the daily incoming solar radiation obtained at Broadfields ($R^2 = 0.94$) for both seasons (Appendix 5). This gave confidence in using the data obtained from Broadfields as a reliable substitute of solar radiation at the experimental site.

5.2.1 Determinants of canopy development

For consistency, the cardinal temperatures used to accumulate Tt were the same as those used in the phenological development study between emergence and silking (Section 4.2.2.4). Air temperature was used to calculate Tt for the regressions with leaf tip and fully expanded leaf appearance. However, for the regression of leaf primordia initiation Tt was calculated based on 50 mm soil temperature (Section 3.7.6.1).

5.2.1.1 Leaf tip appearance

The number of visible leaf tips per plant (Section 3.7.1.1) was related to Tt after emergence by a linear function using least squares regression. By definition all crops had a single leaf tip at emergence. Therefore, regressions were constrained to pass through (0, 1) and calculated individually for each plot. The reciprocal of each gradient is the phyllochron (Section 2.3.1.1). These were then tested for each treatment by ANOVA (Section 3.8).

5.2.1.2 Leaf primordia initiation

The number of leaf primordia on the apices of seedlings taken from each of the 0, 110, and 240 kg P ha^{-1} plots in Experiment 3 (2002/03) (Section 3.7.1.4) was related to Tt after sowing by a linear function using least squares regression for each plot. The plastochron (Tt between successive leaf primordia; °Cd) was calculated as the reciprocal of the gradient of this regression and these were then tested by ANOVA (Section 3.8).

The number of leaf primordia was also regressed against the number of visible leaf tips from the same measured seedlings (Section 3.7.1.4).

5.2.1.3 Fully expanded leaf appearance

The number of fully expanded main stem leaves per plant (Section 3.7.1.1) was related to Tt using an exponential function (Equation 5.1) (Muchow and Carberry, 1989). Coefficients for individual plots were tested using ANOVA (Section 3.8).

$$LN = ae^{(bTt)}$$

Equation 5.1

Where LN= number of fully expanded leaves, a = intercept with Y-axis (leaves), and b represents the degree of curvature (dimensionless).

5.2.1.4 Final leaf number per plant

The final number of main stem leaves per plant was counted at silking and tested across treatments by ANOVA (Section 3.8).

5.2.1.5 Area of Individual leaves

Prior to statistical analyses of leaf area distributions, the area of individual leaves, measured using the Licor 3100 area meter (Section 3.7.1.2), were compared to a second data set of individual leaf areas. This second data set was measured for the analysis of leaf photosynthesis described in Section 6.2.2. This data set was also measured using the Licor 3100 area meter and was collected over a total of 5 days in each of Experiments 1 and 4.

The linear regression in Appendix 10 indicated that the individual leaf area measurements collected in Section 3.7.1.2 was ~20% greater for a given leaf position than the area of an individual leaf at the corresponding leaf position in Section 6.2.2 in Experiment 3. Therefore the area of each individual leaf at each leaf position in Experiment 3 (Section 3.7.1.2) was adjusted using the linear regression in Appendix 10. These adjusted individual leaf area data

were used in subsequent analyses. The regression in Appendix 10 indicated that the individual leaf areas at each position measured in Experiment 1 (Section 3.7.1.2) were consistent with those measured in Section 6.2.2. Consequently the individual leaf area measurements for Experiment 1 were used directly.

The inconsistency of measured individual leaf area between Experiment 3 and that measured in Section 6.2.2 was unclear. Both the data collected in Section 3.7.1.2 and the data collected in Section 6.2.2 were made using the Licor 3100 area meter. However, because the measurements in Section 6.2.2.2 were taken over a range of days these were considered to be more reliable than the measurements in Section 3.7.1.2, which were taken on a single day.

The area of individual leaves (measured in Section 3.7.1.2 for Experiment 1 and the adjusted values in Experiment 3) were then regressed against a bell shaped function of leaf position (numbered acropetally) (Section 3.7.1.2) (Equation 2.3) for individual plots and the coefficients were tested using ANOVA (Section 3.8).

5.2.2 Crop total LAI development

Daily values of TLAI were reconstructed, based on daily accumulated Tt values (Section 4.2.2.4), and the functions for leaf tip appearance, fully expanded leaf appearance and area of individual leaves for each individual plot, using the method of Stone *et al.* (2001b) (Section 2.3.1.4).

The area of fully expanded leaves was predicted by estimating the number of fully expanded leaves from the exponential relationship between Tt and fully expanded leaf number (Section 2.3.1.1). From Leaf 7 this relationship was linearised back to the origin to avoid the artificial

estimation, from the exponential relationship, of approximately two leaves at crop emergence (Figure 5.1). Leaf 7 was used based on the modelling framework of Wilson *et al.* (1995) and the observation that this was when rapid stem elongation began in a range of maize hybrids (Robertson, 1994). The individual area of each of these leaves was estimated from the peaked function (Section 5.3.1.5) and summed to give the fully expanded leaf area per plant.

The expanding leaf area per plant was estimated by assuming that there was a linear increase in the area of each individual leaf from 0 cm^2 at leaf tip appearance to its fully expanded area (determined by the peaked curve) at full leaf expansion. The area of these expanding leaves was summed and added to the fully expanded leaf area per plant to give daily values for PLA. PLA was then multiplied by the mean plant population (Appendix 3) to give crop TLAI. This analysis ignores the interception of solar radiation by tassels. However, the maximum error associated with this assumption is likely to be <10% (Duncan *et al.*, 1967).

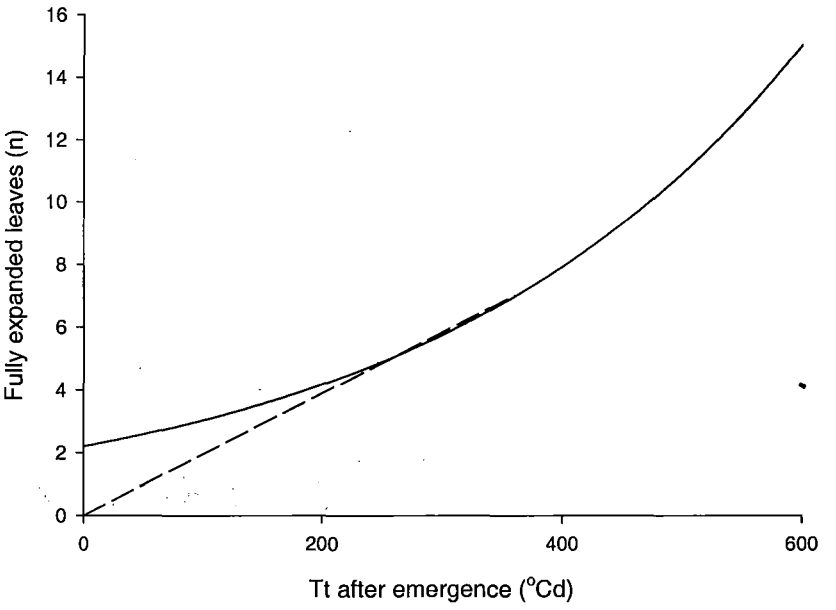

Figure 5.1 Fitted curve (solid line) and linearised curve (dashed line) relating the number of fully expanded leaves to Tt after emergence (T_b=8°C) used when estimating TLAI in sweet corn.

To test the appropriateness of this method, reconstructed TLAI was regressed against measurements of TLAI, made using the LAI-2000 canopy analyser (Section 3.7.2.1). The values of TLAI obtained with the LAI-2000 were not used directly in subsequent analyses because there were insufficient data points to obtain reliable relationships. To accurately determine RI in a crop where LAI is low (≤3) it is necessary to have data points at frequent intervals, and thus the method of reconstructing TLAI was deemed as the most appropriate to obtain the necessary daily values.

Reconstructed TLAI data were fitted to a 3 parameter sigmoid function (Equation 5.2) using least squares regression. The slope of the curve at the inflection point (m) was also derived using Equation 5.3.

$$TLAI = \frac{g}{1+\exp^{(-\frac{days-i}{h})}}$$

Equation 5.2

Where g is the asymptotic value of TLAI, h is a parameter defining the curvature of the function, and i is the position of the inflection point (days).

$$m = \frac{(\frac{1}{h} \times g)}{4}$$

Equation 5.3

The coefficients of these curves and m were then tested using ANOVA (Section 3.8) utilising an orthogonal contrast of crops receiving no fertiliser P against crops receiving fertiliser P (at any rate).

5.2.3 Crop leaf senescence and green LAI

The FSA was quantified for Experiments 1 and 4 by converting the number of senesced leaves per plant (Section 3.7.1.3) to FSA per plant. Because this value was a fraction plant FSA was equivalent to crop FSA.

FSA was related to Tt (T_b = 8 °C) using both a "broken stick" and exponential regressions. In the broken stick model, the parameters of the two line segments were determined using least

squares regression, utilising a series of dummy variables to partition the data to each of the two line segments (Draper and Smith, 1998) with the maximum R^2 used as the criteria for the separation. This analysis assumed that the data points on each line segment did not overlap. There were no differences in the exponential relationships between P treatments therefore a common broken stick regression was fitted to the mean data points for the combined treatments at each sampling date.

Daily estimates of GLAI were calculated, by subtracting FSA from TLAI. FSA was predicted for each day from the two-step regression outlined above and Tt after emergence. Values of GLAI were compared between P treatments at 5 day intervals between crop emergence and final harvest.

5.2.4 Extinction coefficient

The value of k was calculated from Experiment 3 from the exponential relationship (Thornley and Johnson, 2000) (Section 2.3.1) between RI_{frac} and TLAI using least squares regression. The exponential relationship was calculated until the last leaf had fully expanded to avoid skewing the data. Similarly, RI_{frac} was related to TLAI (and not GLAI) because senesced leaves also intercept radiation.

5.2.5 Calculated radiation interception

Values of k were used to calculate daily RI_{frac} from GLAI in both Experiments 1 and 4. The daily values of RI_{frac} were multiplied by the total daily incident solar radiation (MJ m^{-2}) measured at Broadfields' meteorological station (Appendix 11) to give daily solar radiation interception. These daily values were then summed to give RI_{cum} for each plot.

The calculated values of RI_{cum} for individual plots were regressed against days after crop emergence using a 3-parameter logistic curve (Equation 5.4). This curve was fitted to days after emergence rather than Tt on the basis that it was the number of days that the canopy is green for that is important in determining radiation interception. Calculating radiation interception based on Tt would be inappropriate because there is likely to be a strong correlation between daily mean temperature and incoming solar radiation.

$$RI_{cum} = \frac{p}{1+(\frac{x}{r})^q}$$

Equation 5.4

Where p = the theoretical maximum value of RI_{cum} (MJ m^{-2}), q = the curvature of the function, and r = the midpoint of the curve (days).

From these curves the duration of the lag phase (emergence until 10% of maximum RI_{cum} was obtained) and the rate of linear increase (from the end of the lag phase to crop harvest) were calculated. Crops were harvested before physiological maturity and consequently the asymptote of the relationship between RI_{cum} and days after emergence (Equation 5.4) was not obtained. Maximum RI_{cum} (at crop harvest), the duration of the lag phase, and the rate of linear increase were then tested using ANOVA (Section 3.8) utilising an orthogonal contrast of crops receiving no fertiliser P with crops receiving fertiliser P (at any rate).

5.2.5.1 Sensitivity analysis

A sensitivity analysis was used to distinguish the relative effects of leaf appearance rate (leaf tips and fully expanded leaves) and individual leaf area on final RI_{cum} in response to P

fertiliser. Simulations of RI_{cum} using leaf appearance and leaf area of the 0 kg P ha^{-1} crop; leaf appearance and leaf area of 200/240 kg P ha^{-1} crop; leaf appearance from 0 kg P ha^{-1} crop with leaf area of 200/240 kg P ha^{-1} crop; and leaf appearance from 200/240 kg P ha^{-1} crop with leaf area from 0 kg P ha^{-1} crop were run to predict the effect of each variable both together and separately on final calculated RI_{cum}.

Simulations were made using the approach used above to estimate RI_{cum}, by reconstructing TLAI and GLAI. These simulations were run for both seasons. Predicted values of RI_{cum} were compared between the theoretical crops on the date of harvest of the earliest crop to mature.

5.3 Results

5.3.1 Determinants of canopy development

5.3.1.1 Leaf tip appearance

There was a positive linear relationship (R^2> 0.95) between the number of visible leaf tips and Tt in both seasons (Figure 5.2a b). There was an acceleration ($p<0.01$) in the rate of leaf tip appearance with increasing P fertiliser. In 2001/02 the phyllochron decreased from 35.0 °Cd for crops receiving no P to 29.0 °Cd when 200 kg P ha^{-1} was applied (Figure 5.2c). The phyllochron also decreased in 2002/03 from 29.7 °Cd with no P fertiliser to 25.4 °Cd with 240 kg P ha^{-1} (Figure 5.2d).

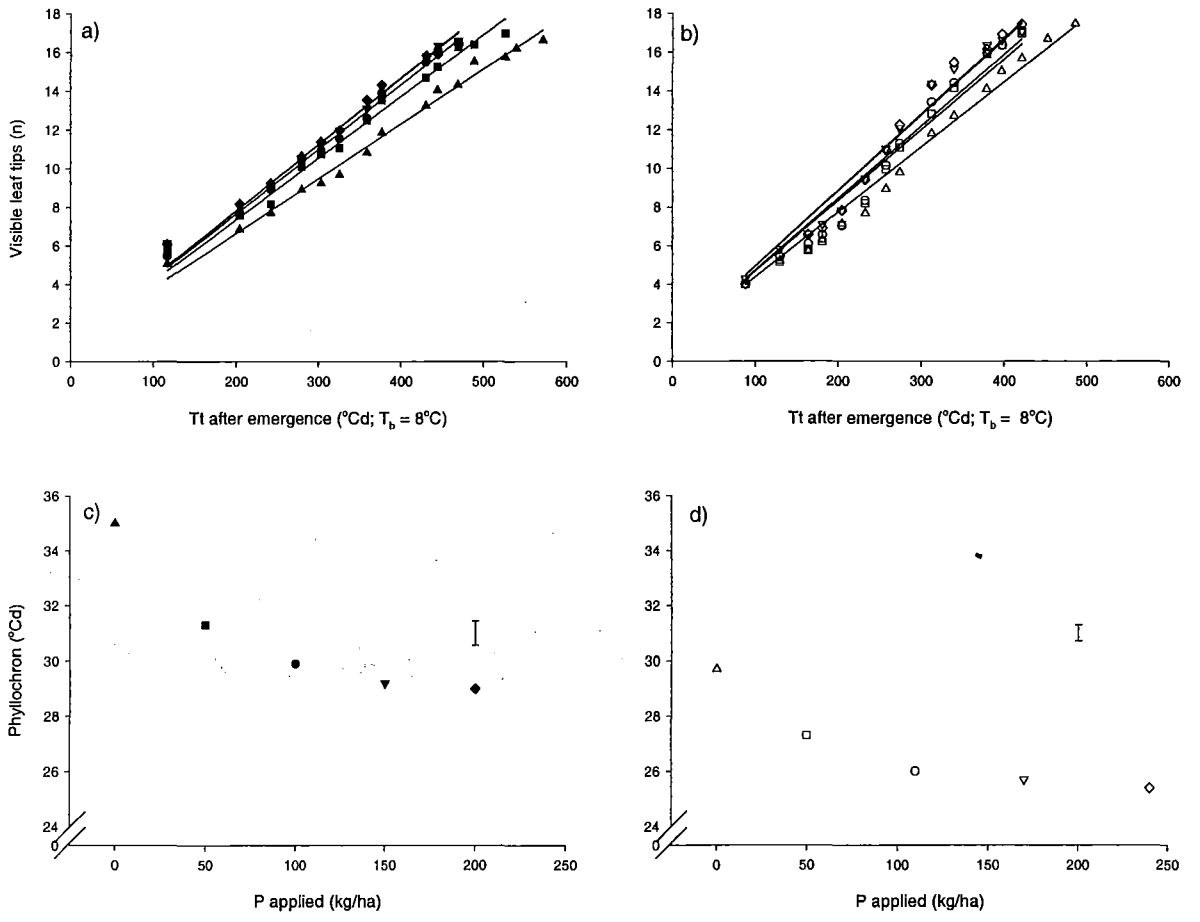

Figure 5.2 Number of visible leaf tips for 'Challenger' sweet corn against Tt (°Cd after emergence, T_b = 8°C) for crops grown with different P fertiliser rates in 2001/02 (a) and 2002/03 (b); and phyllocrons, calculated from these regressions, in 2001/02 (c) and 2002/03 (d). (Symbols in Table 4.1). (Error bars represent pooled s.e of the mean).

5.3.1.2 Initiation of leaf primordia (plastochron)

The number of leaf primordia was linearly related to Tt after sowing (T_b= 8 °C; based on 50 mm soil temperature) and the plastochron ranged from 29.1°Cd for 0 kg P ha^{-1} crops to 26.7 °Cd for crops receiving 240 kg P ha^{-1} (Figure 5.3). By the final sampling on 22 December

2002 (~472 °Cd after sowing) all plants had 16 leaf primordia and had initiated tassel primorida at the apex.

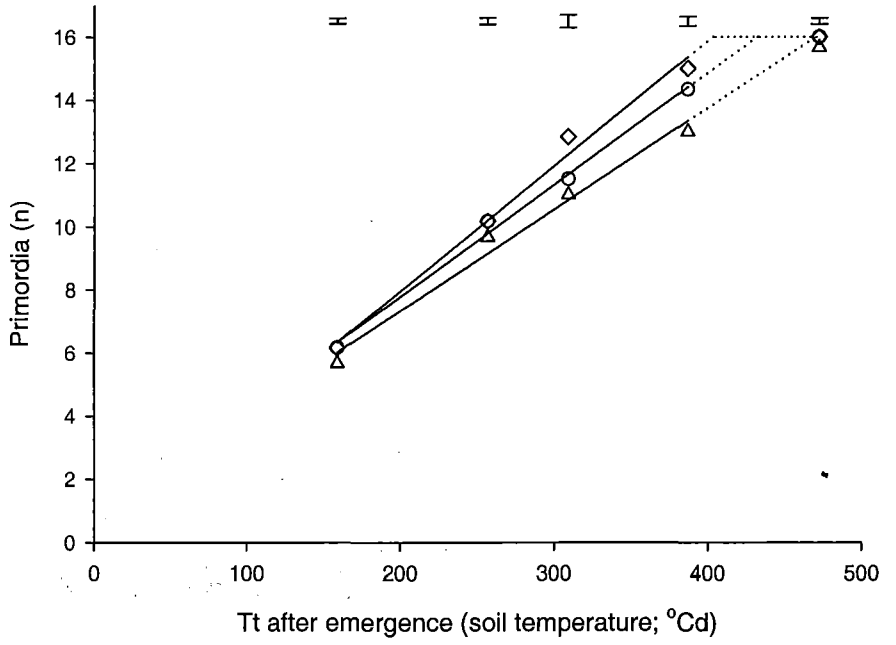

Figure 5.3 Number of leaf primordia on apices of 'Challenger' sweet corn against Tt after sowing (T_b = 8°C) for crops receiving three rates of P fertiliser (Symbols in Table 4.1) when grown at Lincoln, Canterbury, New Zealand in 2002/03. Solid lines represent linear regressions based on first four data points. Dotted lines are between 387 and 472 °Cd and are not included in the regressions because all plants had tassel primordia at 472 °Cd. The error bars represent the pooled standard error of the treatment means for each sample date.

As expected there was a strong linear (R^2= 0.98) relationship between the number of individual leaf tips and the number of initiated leaf primordia on the apex. For each leaf primordium initiated at the apex 0.58 visible leaf tips appeared (Figure 5.4).

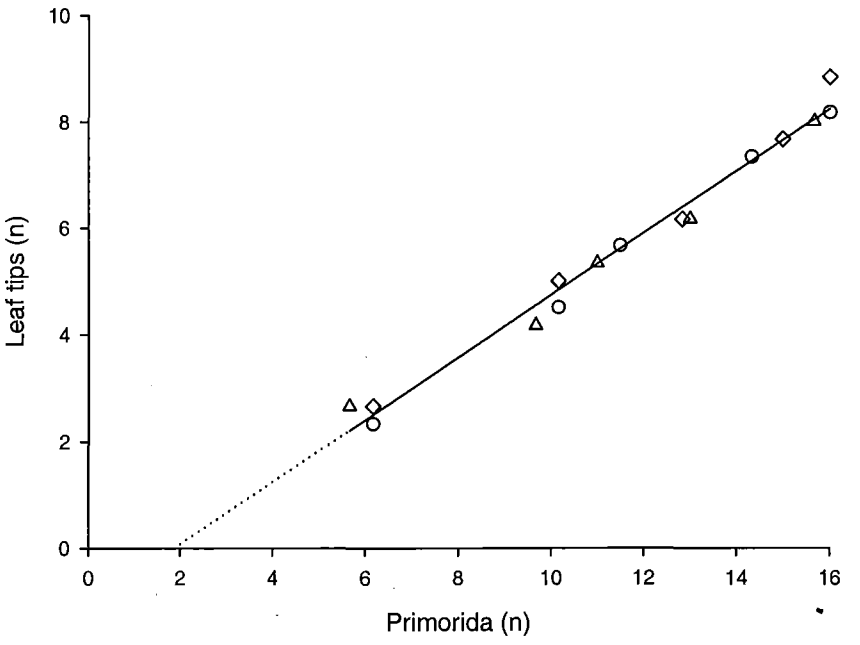

Figure 5.4 Number of visible leaf tips against number of leaf primordia on the apex of 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2002/03 at three rates of fertiliser P (Symbols in Table 4.1). Regression equation: y = 0.58 (±0.02) x – 1.09 (±0.26); R^2 = 0.98.

5.3.1.3 Fully expanded leaf appearance

There was an exponential relationship (R^2> 0.96) between the number of fully expanded leaves and Tt after emergence for all treatments (Figure 5.5 a and b). In 2002/03 there was a strong indication that between the first and 7th fully expanded leaves the relationship was linear (Figure 5.5 b). In subsequent analyses of TLAI, GLAI and RI_{cum} this was addressed using the method outlined in Section 5.2.2 (Figure 5.1). Fertiliser P had no effect on the intercept (a) of the relationship. However, the degree of curvature in the relationship was greater ($p<0.05$) when P was applied in both seasons (Table 5.1). This indicates that fully expanded leaves appeared at a faster rate in P fertilised crops.

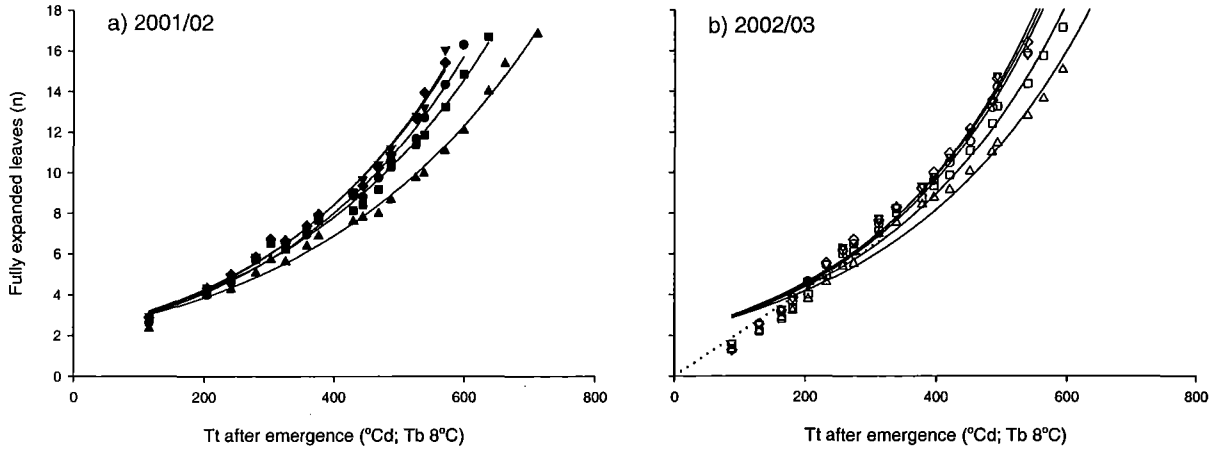

Figure 5.5 Number of fully expanded leaves against Tt after emergence (T_b= 8°C) for 'Challenger' sweet corn grown at Lincoln, Canterbury, New Zealand in 2001/02 (a) and 2002/03 (b) at five fertiliser P levels. (Symbols in Table 4.1) The dotted line in 2002/03 represents the theoretical relationship between leaves 0 and 7. Fitted curves are from Equation 5.1 and the coefficients are given in Table 5.1.

Table 5.1 Coefficients of Equation 5.1 for the relationship between the number of fully expanded leaves and Tt (T_b=8°C) after emergence for 'Challenger' sweet corn grown with different rates of P fertiliser at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03.

2001/02	Y intercept	Curvature	2002/03	Y intercept	*Curvature*
kg P ha^{-1}	(a)	(b)	kg P ha^{-1}	(a)	(b)
0	2.1	0.0030 a*	0	2.2	0.0033 a
50	2.2	0.0032 ab	50	2.1	0.0036 ab
100	2.0	0.0034 bc	110	2.1	0.0038 bc
150	2.1	0.0035 c	170	2.1	0.0040 c
200	2.2	0.0034 bc	240	2.1	0.0039 bc
s.e.	0.04	0.00008	s.e.	0.07	0.00032

s.e. = pooled standard error of the mean.
*Values followed by the same letter within a season are not significantly different ($\alpha<0.05$).

5.3.1.4 Final number of leaves

In 2001/02 crops receiving 0 kg P ha^{-1} (18.0 leaves) had 1.3 more ($p<0.01$) main stem leaves than crops receiving 200 kg P ha^{-1} (16.7 leaves) (Figure 5.6 a), while in 2002/03 there were no differences in the final number of main stem leaves (17.2 leaves) (Figure 5.6 b).

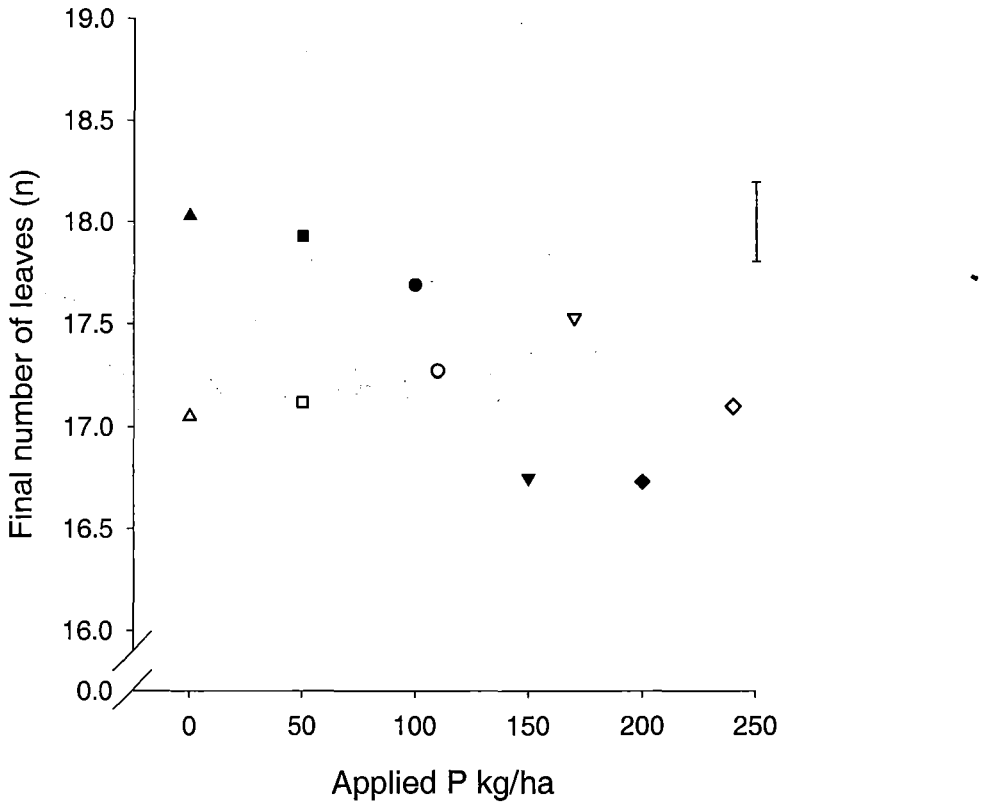

Figure 5.6 Final number of main stem leaves for 'Challenger' sweet corn in response to five P fertiliser rates (Symbols in Table 4.1) in 2001/02 and 2002/03 at Lincoln, Canterbury, New Zealand. Error bar represents pooled s.e of the mean for both seasons.

5.3.1.5 Individual leaf area

A four parameter bell shaped function (Equation 2.3) described ($R^2= 0.99$) the relationship between the area of individual leaves and main stem leaf position (Figure 5.7). The area of the largest leaf (Y_0) increased ($p<0.05$) with the addition of P fertiliser in both seasons (Table 5.2). In 2001/02 (Experiment 1) crops receiving no P fertiliser had Y_0 of 415 cm^2 compared

with 570 cm^2 in the 200 kg P ha^{-1} crops. In 2002/03 Y_0 was 420 cm^2 for the 0 kg P ha^{-1} crop and ≥500 cm^2 with P rates ≥110 kg P ha^{-1} (Table 5.2).

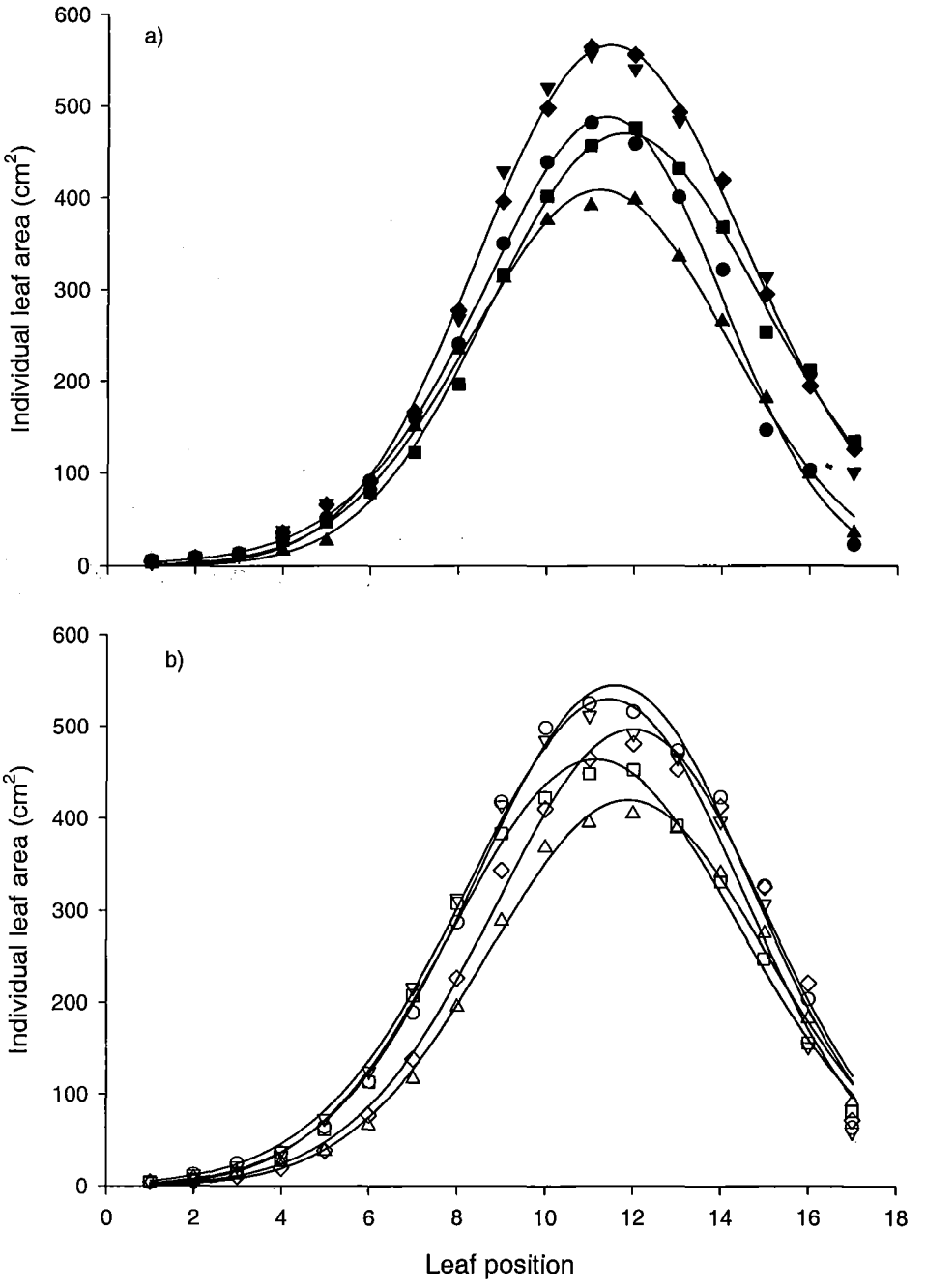

Figure 5.7 Fitted curves (Equation 2.3) of mean individual leaf area against main stem leaf position for 'Challenger' sweet corn in 2001/02 (a) and 2002/03 (b) in response to five rates of fertiliser P (Symbols in Table 4.1) grown at Lincoln, Canterbury New Zealand. The coefficients of these curves are provided in Table 5.2.

Table 5.2 Coefficients of the bell shaped curve between the area of individual leaves and main stem leaf position (Equation 2.3) for 'Challenger' sweet corn grown at differing rates of fertiliser P at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03.

Treatment (kg P ha^{-1})	*Area of the largest leaf* Y_0 *(cm^2)*	*Position of the largest leaf* X_0 *(n)*	*Breadth of the peak* c	*Skew of the curve* d
2001/02				
0	415 a*	11.1	0.06	$-3.0*10^{-4}$
50	475 a	11.7	0.05	$1.0*10^{-3}$
100	487 ab	11.4	0.06	$-1.4*10^{-3}$
150	567 b	11.4	0.05	$9.0*10^{-4}$
200	570 b	11.6	0.06	$-6.0*10^{-4}$
s.e.	27.4	0.16	0.004	$9.0*10^{-4}$
2002/03				
0	421 a	11.8	0.05	$7.0*10^{-4}$
50	472 ab	11.2	0.05	$<1.0*10^{-4}$
110	543 b	11.5	0.05	$-4.0*10^{-4}$
170	530 b	11.4	0.05	$-1.5*10^{-3}$
240	499 b	11.9	0.05	$<1*10^{-4}$
s.e.	23.4	0.25	0.003	$8.0*10^{-4}$

* Values within a column followed by the same letter are not significantly different ($\alpha>0.05$).

The value of X_0 was consistently between leaf 11 and 12 in all treatments in both seasons (Table 5.2). This indicates that the leaves at positions 11 and 12 were the largest and approximately the same size. Similarly, fertiliser P had no effect on the skewness or kurtosis of the curves in either season (Table 5.2).

5.3.2 Total LAI

Calculated TLAI values were consistent (R^2=0.78) with an independent data set measured with the LAI-2000 canopy analyser (Section 3.7.2.1) (Figure 5.8). Calculated values of TLAI (Section 5.2.2) were consistently lower than measured values of TLAIs >2.0. This indicated a systematic error in either the calculated or measured TLAI values, probably as a result of the emergence of tassels and stems as crops approached anthesis. These were not included in the calculated values of TLAI.

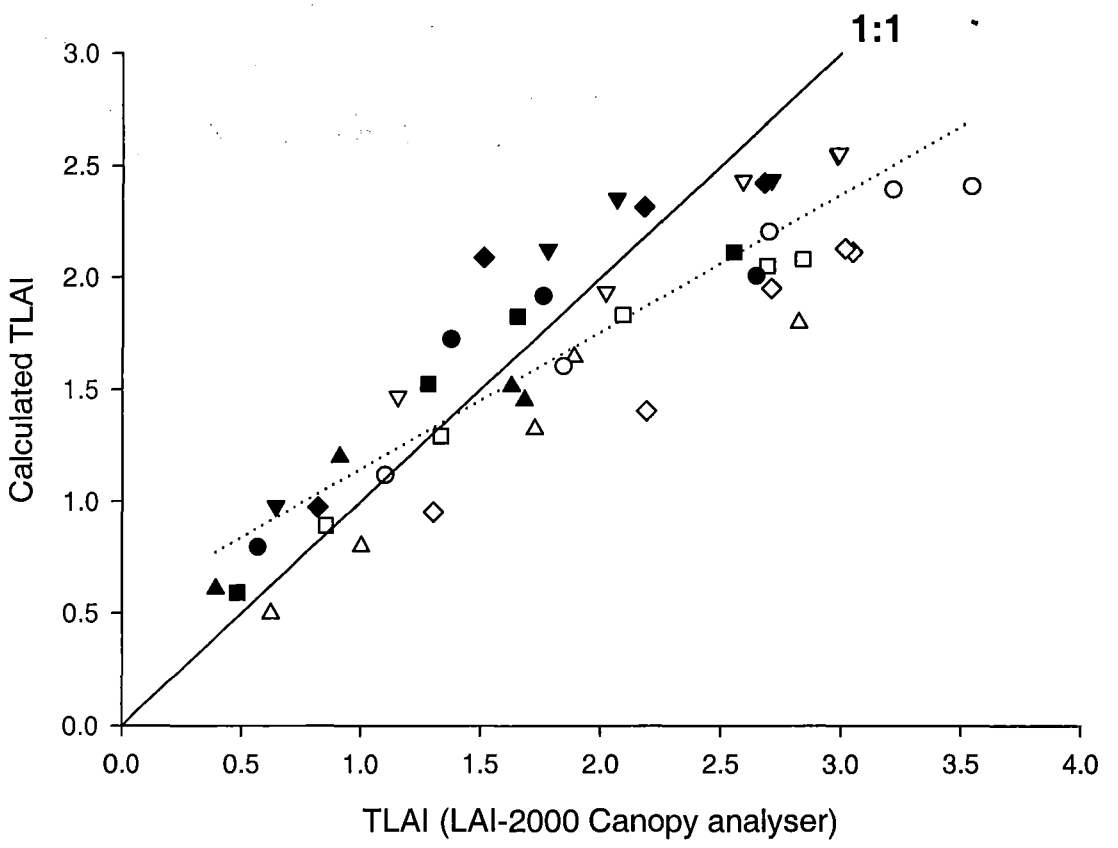

Figure 5.8 Calculated total leaf area index (TLAI) against TLAI obtained using the LAI-2000 canopy analyser for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand at five rates of P fertiliser. (Symbols in Table 4.1). Regression : $y = 0.53 + 0.61x$, R^2=0.78.

Calculated TLAI followed a sigmoid pattern (Equation 5.2) over time (Figure 5.9). Maximum calculated TLAI increased from 1.7 without P fertiliser to 2.4 with 200 kg P ha^{-1} in 2001/02. In 2002/03 maximum calculated TLAI increased from 1.8 without P fertiliser to 2.6 with 170 kg P ha^{-1} (Table 5.3). The orthogonal contrasts in both seasons indicated that crops receiving any rate of fertiliser P had a greater ($p<0.05$) maximum TLAI than crops receiving no fertiliser P.

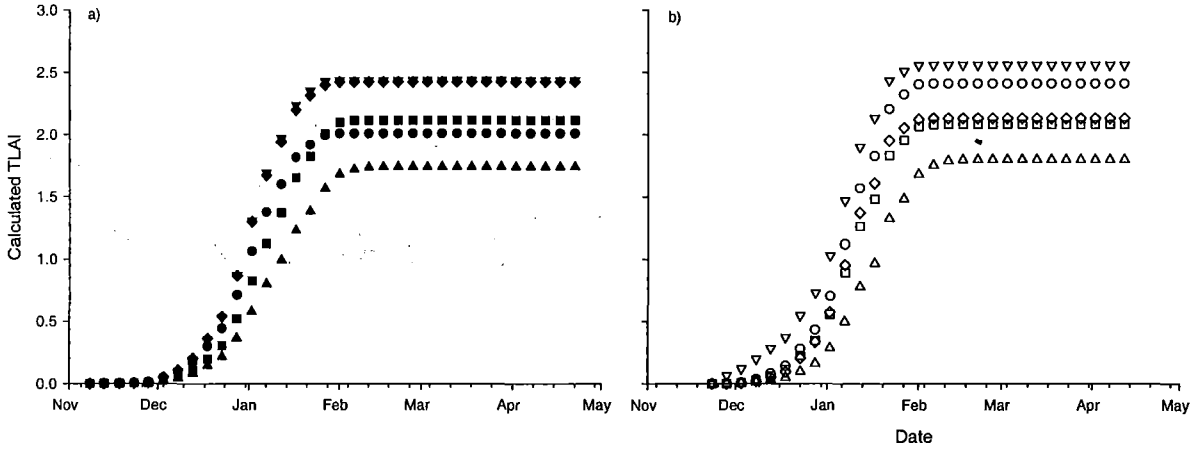

Figure 5.9 Temporal changes in calculated TLAI for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/02 (a) and 2002/03 (b) in response to five rates of fertiliser P (Symbols in Table 4.1).

Table 5.3 Coefficients of Equation 5.2 between calculated TLAI (Section 5.2.2) and days after emergence for 'Challenger' sweet corn grown at differing rates of fertiliser P at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03.

Treatment kg P ha^{-1}	*Maximum TLAI*	*Inflection point (days)*	*Slope at inflection point (TLAI* day^{-1}*)*	*Curvature parameter*
	(g)	**(i)**	**(m)**	**(h)**
2001/02				
0	1.8	63	0.05	8.8
50	2.1	60	0.12	6.1
100	2.0	55	0.07	7.5
150	2.4	55	0.09	7.2
200	2.4	55	0.16	5.3
significance	<0.1*	<0.05	n.s.	n.s.
s.e.	0.17	1.4	0.038	1.1
2002/03				
0	1.8	52	0.06	7.7
50	2.1	48	0.07	7.3
110	2.4	47	0.15	5.3
170	2.6	43	0.38	5.9
240	2.1	48	0.8	6.5
significance	<0.1*	<0.05	n.s.	n.s.
s.e.	0.16	1.5	0.140	1.5

* Orthogonal contrast between control (0 kg P ha^{-1} crops) and crops receiving P fertiliser was statistically significant ($\alpha<0.05$)
s.e. is pooled standard error of the mean.

5.3.3 Leaf senescence and GLAI

Patterns of FSA did not differ among treatments so grand means were used in each season. Exponential, and two-step linear relationships fitted for FSA against Tt produced a regression with an $R^2 \leq 0.97$. However, a gap in the data taken between 400 and 800 °Cd in 2001/02

meant the slope of the second line was heavily dependent on the final three data points (Figure 5.10).

The broken stick models showed a break point (where FSA began to increase rapidly) at 821 °Cd in 2001/02 and 478 °Cd in 2002/03. At Tt less than these points FSA was minimal (i.e. <0.05). In 2001/02 for every 100°Cd increase in Tt above 821°Cd FSA increased by 0.12. Whereas in 2002/03 for every 100°Cd increase above 478°Cd FSA increased by 0.038 (Figure 5.10). These broken stick models of FSA in response to Tt after emergence were used in subsequent analyses of GLAI and RI_{cum}.

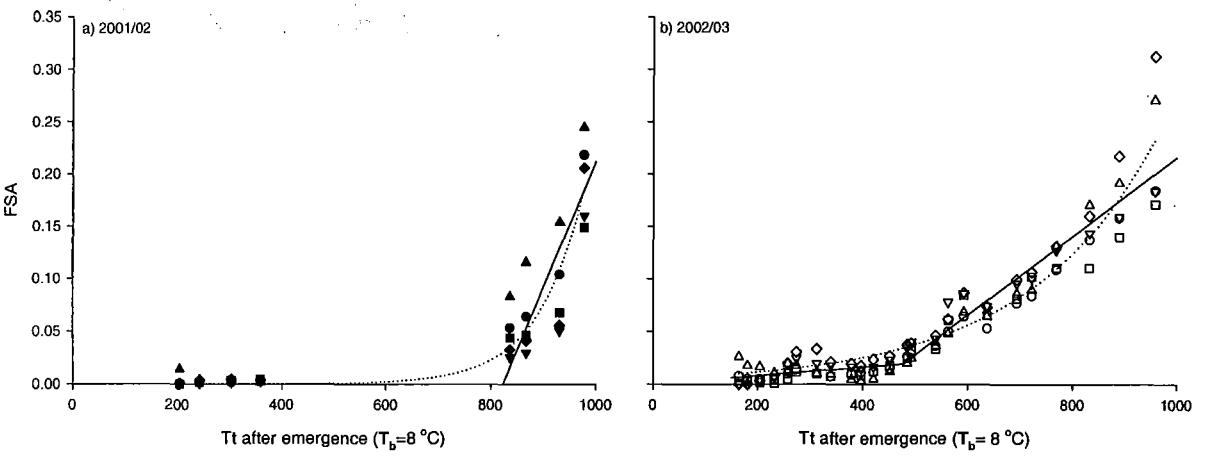

Figure 5.10 Fraction of senesced leaf area (FSA) against Tt after emergence (T_b= 8°C) for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/02 (a) and 2002/03 (b). (Symbols in Table 4.1). In each case the dotted line represents the fitted exponential equation: a) y = e (0.0119*x) ; R^2= 0.97; b) $y=0.0051*e^{[0.004*x]}$; R^2 = 0.98; and the solid line represents the two stage linear model: a) $y=(4.0x10^{-6})*x$ (x<821°Cd), y = 0.0012*x-0.99 (x>821°Cd); R^2= 0.90 b) $y=0.00004x$ (x<478°Cd), y = 0.00038x-0.161 (x>478°Cd); R^2=0.97.

As expected the calculated GLAI (Figure 5.11) showed the same pattern as TLAI until the FSA break points, after which GLAI decreased.

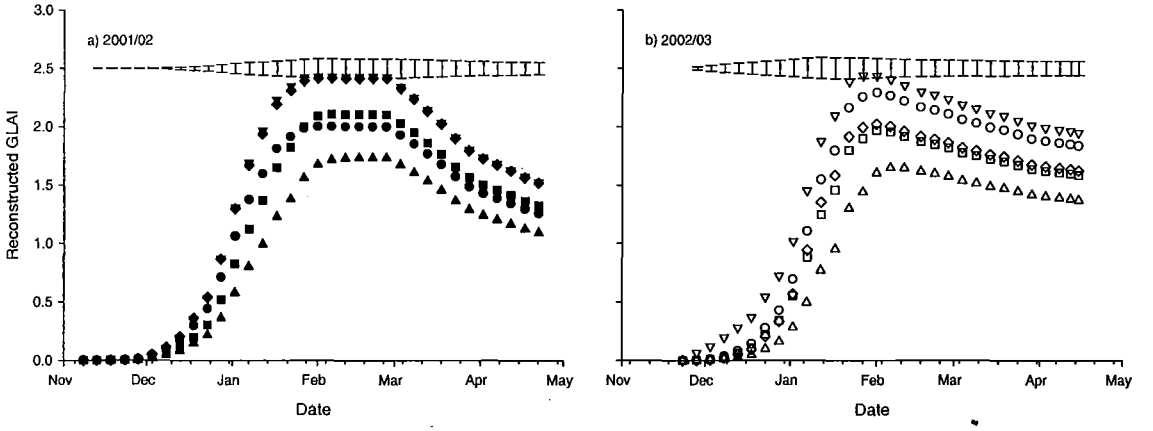

Figure 5.11 Temporal changes in calculated GLAI for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/02 (a) and 2002/03 (b) at different rates of P fertiliser. (Symbols in Table 4.1). For clarity data are presented at five day intervals. Error bars represent pooled s.e. of the mean.

5.3.4 Radiation interception

5.3.4.1 Extinction coefficient

The exponential regression of RI_{frac} against calculated TLAI showed k = 0.65 (R^2=0.90) for both treatments (Figure 5.12). This indicated that critical LAI (LAI_{crit}; where 95% of solar radiation is intercepted) was 4.6.

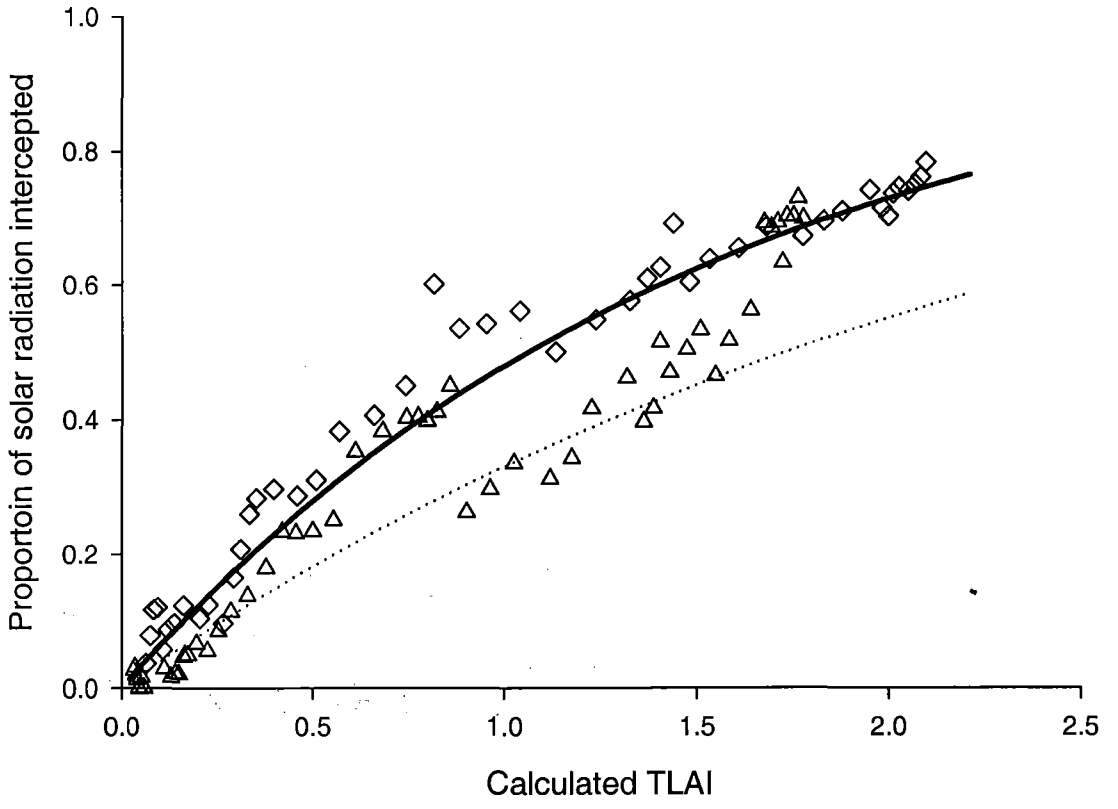

Figure 5.12 Proportion of solar radiation intercepted against TLAI until maximum TLAI for 'Challenger' sweet corn grown at Lincoln, Canterbury, New Zealand in 2002/03 with 0 (Δ) or 240 (◊) kg P ha^{-1}. Solid line is fitted regression $y = 1 - e^{(-0.653x)}$; $R^2 = 0.90$. Dotted line is $y = 1 - e^{(-0.4x)}$ (Muchow and Sinclair 1990), and is included for comparison.

5.3.4.2 Cumulative radiation interception

Using k= 0.65 (Figure 5.12), GLAI (Figure 5.11), and daily incoming solar radiation (Appendix 11), RI_{cum} was calculated on a daily basis. A logistic growth curve (Equation 5.4) was fitted (R^2>0.99) to RI_{cum} against days after emergence in both 2001/02 and 2002/03. The strength of this fit is somewhat artificial because it represents reconstructed values of GLAI and a constant k. A more appropriate measure of the variation in this curve can be obtained from observing the variation in the relationship between TLAI and daily RI_{frac} (Figure 5.12).

Total RI_{cum} at harvest was greater ($p<0.05$) in plots receiving P (at any rate) than crops receiving no P for both seasons. In 2001/02 crops receiving no P intercepted a total of 970 MJ m^{-2}, whereas sweet corn that received 200 kg P ha^{-1} intercepted 1175 MJ m^{-2} in total (Figure 5.13 a). In 2002/03 the 0 kg P ha^{-1} control crops intercepted a total of 1040 MJ m^{-2}, whereas crops receiving P fertiliser intercepted between 1200 and 1450 MJ m^{-2} (Figure 5.13 b). The higher total RI_{cum} in P fertilised crops was caused by both a reduction in the duration of the lag phase and an increase in the linear rate of RI_{cum} accumulation (Table 5.4).

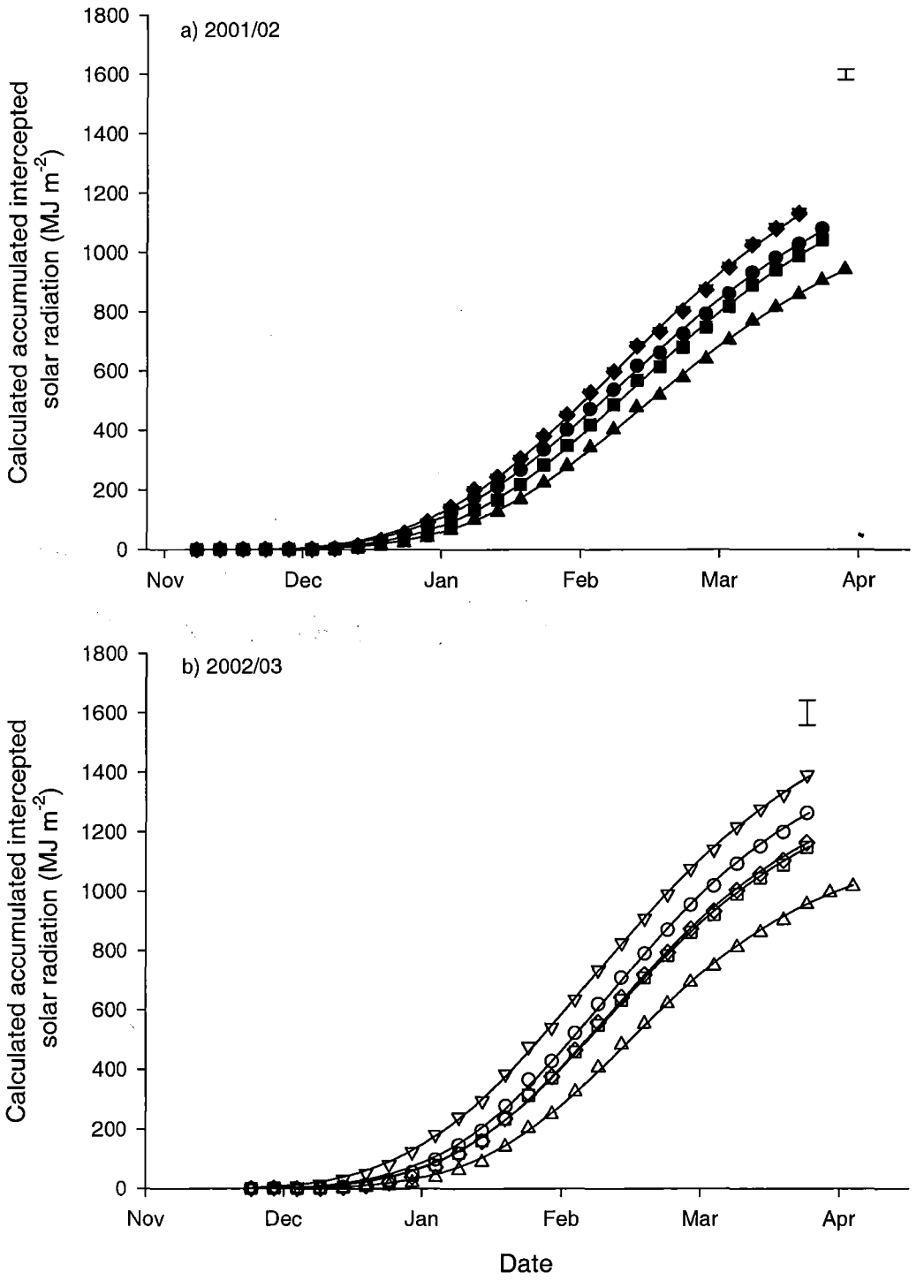

Figure 5.13 Time course of calculated accumulated intercepted solar radiation by 'Challenger' sweet corn grown at five P fertiliser rates (Symbols in Table 4.1) in 2001/02 (a) and 2002/03 (b) at Lincoln, Canterbury New Zealand. Fitted curves are Equation 5.4. Error bars represent pooled s.e. of the mean for accumulated intercepted radiation at final harvest.

Table 5.4 Calculated variables of Equation 5.4 between RI_{cum} (Section 5.2.5) and days after emergence for 'Challenger' sweet corn grown at differing rates of fertiliser P at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03.

Treatment (kg P ha^{-1})	*Total RI_{cum} at harvest (MJ m^{-2})*	*Duration of lag phase (days)*	*Linear rate of increase of RI_{cum} (MJ m^{-2} day^{-1})*
2001/02			
0	969	60	10.3
50	1067	57	11.8
100	1113	53	11.6
150	1192	53	12.9
200	1176	52	12.8
significance	<0.05	<0.01	<0.05
s.e.	35.5	1.2	0.45
2002/03			
0	1036	52	11.3
50	1199	46	13.2
110	1305	44	14.5
170	1447	40	14.8
240	1216	46	13.3
significance	<0.1*	<0.1*	<0.05
s.e.	83.1	2.5	0.6

* Orthogonal contrast between control (0 kg P ha^{-1} crops) and crops receiving P fertiliser was statistically significant (α<0.05)
s.e. is pooled standard error of the mean.

5.3.4.3 Relative effects of leaf appearance and leaf area on predicted RI_{cum}

Both the reduced leaf appearance rate (leaf tips and fully expanded), and reduced individual leaf area of sweet corn crops receiving no P fertiliser contributed to the lower values of RI_{cum} (Table 5.5). The reduced area of individual leaves caused the greatest reduction in RI_{cum} in 2001/02 but the reduced leaf appearance rate was the greater cause in 2002/03 (Table 5.5). In

2001/02, the percentages of RI_{cum} compared with the 200 kg P ha^{-1} crop in 2001/02 were 76% when both the slower leaf appearance rate and reduced area of individual leaves were used, 91% when only the slower leaf appearance rate was used, and 85% when only the reduced area of individual leaves was used. The respective values of these same simulations relative to the 240 kg P ha^{-1} crop in 2002/03 were 79%, 87% and 91%.

Table 5.5 Sensitivity analyses of the simulated effects on accumulated solar radiation interception, of reduced individual leaf area and reduced leaf appearance rate with no P fertiliser, in 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03.

Simulated treatment	*Simulated final* RI_{cum} *(MJ* m^{-2}*).*	*% fully fertilised crop*
2001/02		
0 kg P ha^{-1} (leaf appearance and leaf area reduced)	903	76%
0 kg P ha^{-1} (leaf appearance only reduced)	1077	91%
0 kg P ha^{-1} (leaf area only reduced)	1002	85%
200 kg P ha^{-1}	1184	100%
2002/03		
0 kg P ha^{-1} (leaf appearance and leaf area reduced)	1010	79%
0 kg P ha^{-1} (leaf appearance only reduced)	1120	87%
0 kg P ha^{-1} (leaf area only reduced)	1165	91%
240 kg P ha^{-1}	1287	100%

5.4 Discussion

5.4.1 Radiation interception and GLAI development

It is likely that most of the increase in crop DM with P fertiliser observed in both seasons (Figure 4.1c) was due to the increased RI_{cum} (Figure 5.13). RI_{cum} increased when P fertiliser was applied due to a faster rate of appearance of fully expanded leaves and leaf tips and also an increased area of individual leaves. The faster rate of leaf appearance (Figure 5.2 and Figure 5.5) when P was applied meant that the establishment of the canopy was faster in these crops. This more rapid rate of canopy expansion was reflected in the shorter lag phase of RI_{cum} when P fertiliser was applied (Table 5.4). The increased area of individual leaves (Figure 5.7) when P fertiliser was applied resulted in an increased maximum GLAI (Figure 5.11) in these crops. This meant that the crops which were given P fertiliser intercepted a greater proportion of the incident solar radiation (Figure 5.12) during the major part of crop growth. This was reflected in the greater linear rate of RI_{cum} accumulation in crops receiving P fertiliser (Table 5.4).

These results were consistent with those of Plenet *et al.* (2000b) in maize crops where RI_{cum} was ~10% less in maize crops receiving no P compared with those receiving 53 or 111 kg P ha^{-1}. However, their reduction in RI_{cum} was almost exclusively due to a delay in canopy development with no apparent effect on the subsequent linear rate of RI_{cum} accumulation. The delay in canopy expansion was the effect of a reduced leaf appearance rate, similar to that found here in both seasons. Maximum GLAI was also reduced in the maize crops (Plenet *et al.*, 2000b). For example in 0 kg P ha^{-1} control crops GLAI reached a maximum of ~5, and crops receiving P fertiliser had a maximum GLAI of ~6 (Plenet *et al.*, 2000b). However, because both of these values were above the LAI_{crit} of 4.6 (Figure 5.12) there was no effect on the linear rate of accumulation of RI_{cum}. Using a k of 0.65 RI_{frac} would be estimated as 0.98 and 0.96 for GLAI of 6 and 5 respectively. This difference would have a negligible effect on

the accumulation of RI_{cum}. In contrast, in the current experiments GLAI was ~ 1.7 and 2.5 for 0 and 200/240 kg P ha^{-1} treatments in both years. With these values, RI_{frac} would have been 0.67 and 0.80 for GLAIs of 1.7 and 2.5 respectively. This would have had a profound effect on the linear rate of RI_{cum} accumulation (Figure 5.13).

The results of Plenet *et al.*, (2000b) and those from the current experiments suggest that the delay in canopy development could occur in all P deficient *Zea mays* crops. However, the effect on the linear rate of accumulation is more important in short season environments, where maximum GLAIs are normally low ($\leq$3) due to the use of shorter duration varieties with fewer and smaller leaves (Sorensen and Stone, 1999). In this case any decrease in maximum GLAI caused by P deficiency, will have a major effect on RI_{frac} and hence the linear rate of RI_{cum} accumulation will be markedly reduced.

The sensitivity analysis (Table 5.5) confirmed that both the slower leaf appearance rates and reduced individual leaf areas were pivotal in determining the reduced total RI_{cum} in the present study.

5.4.2 GLAI and extinction coefficient

Canopy architecture was unaffected by P, and hence k did not change (Figure 5.12). Therefore, the reduction in RI_{cum} (Figure 5.13) in P deficient sweet corn crops was solely the product of decreases in GLAI. The k of 0.65 determined here is similar to a previously reported value in maize (Monteith, 1969) and is consistent with the larger values of k reported at higher latitudes (Section 2.3.1). However, it is greater than a commonly used value of 0.4 (Muchow *et al.*, 1990), measured in a sub-tropical environment. This has important implications for the prediction of RI_{cum}, particularly in the current experiments where GLAI for all treatments was < LAI_{crit} (Figure 5.11). When GLAI< LAI_{crit}, the value of k is important

in determining RI_{frac}. Consequently, using an assumed k of 0.4 would have given marked underestimates of RI_{cum} in the current experiments. For example, in 2001/02 an assumed extinction coefficient of 0.4 would have resulted in RI_{cum} of 705 MJ m^{-2} (c.f. 970 MJ m^{-2} using k = 0.65) in the 0 kg P ha^{-1} crops and 905 MJ m^{-2} (c.f 1175 MJ m^{-2} using k = 0.65) in the 200 kg P ha^{-1} crops. Using k = 0.4 would have led to a value of calculated RI_{cum} at final harvest which may have under-estimated RI_{cum} by ~25%. Consequently, where an assumed k of 0.4 has been used estimated values of RI_{cum} may be incorrect (e.g. Stone *et al.*, 2001a).

The plant populations used in these experiments are consistent with current practices in commercial sweet corn crops in New Zealand. Given that calculated GLAI's in the current study and that of (Stone *et al.*, 2001b) were low, there is potential that RI_{cum} and hence kernel yield may be increased by an increase in plant populations. However, caution must be applied to increasing plant population, as a large increase in plant population may lead to a reduction in the number of harvestable ears $plant^{-1}$ and hence economic yield may decrease. The data in Figure 2.8 demonstrates that a decrease in yield per plant can be expected to be associated with an increased unfilled tip length, and therefore the proportion of harvestable ears may fall. However, this is an area of research that requires further examination.

5.4.3 LAI determinants

5.4.3.1 Leaf appearance

The rate of leaf tip appearance increased in crops that were supplied with P fertiliser (Figure 5.2). It is difficult to distinguish between an effect of P nutrition on leaf primordium initiation and a limitation of extension of leaf primordia into visible leaf tips.

The preliminary data collected in 2002/03 showed that the plastochron decreased from 29.1 °Cd without P fertiliser to 26.7°Cd in crops receiving 240 kg P ha^{-1} (Figure 5.3). This

indicates that the rate of leaf primordium initiation was faster in crops supplied with P. Similarly, Jacobs and Pearson (1992) found plastochrons of 17.8 °Cd and 14.5 °Cd (T_b=10°C) in field grown maize receiving 0 or 30 kg N ha^{-1} per week respectively. The 0 kg N ha^{-1} per week plants had a decreased relative growth rate of the apical dome compared with the 30 kg N ha^{-1} per week plants. This implies a growth limitation of the apex for leaf primordium initiation.

Regression analysis showed a strong relationship (R^2 = 0.98) between the number of leaf tips and the number of primordia (Figure 5.4). This has been demonstrated previously in wheat (Kirby, 1990) and oats (Sonego *et al.*, 2000).

These results point to a minor direct physiological effect of P on leaf initiation and a major effect of assimilate supply on the extension of primordia to become visible leaf tips. Rodriguez *et al.* (1998a) determined that the increased phyllochron of P deficient wheat was due to both an increased plastochron and a slower rate of leaf extension.

The hypothesis that the reduced rate of leaf tip appearance under P deficiency was caused by a reduction in assimilate supply is supported by the results of Birch *et al.* (1998d), where field grown maize had a longer phyllochron under shaded conditions (Section 2.3.1.1). There is probably a more general effect of assimilate supply (in the current experiments limited by P) limiting leaf tip appearance. The hypothesis of McMaster *et al.* (2003) that environmental factors other than temperature exert a major effect on the cell expansion and elongation of un-emerged leaf primordia is consistent with this interpretation.

Fully expanded leaf appearance followed an exponential relationship with Tt in both seasons (Figure 5.5). This was due to the later leaves, i.e. leaves 12 onwards, appearing at a faster rate as the apex emerged from the soil and rapidly elongated (Section 2.3.1). This elongation was more rapid in crops receiving fertiliser P compared with a P deficient crop, probably caused by a decreased growth rate in these crops. As a consequence later leaves were not 'pushed' out as rapidly from the stem apex in the P deficient crops.

5.4.3.2 Individual leaf area

The area of individual leaves was described accurately by a bell-shaped function (Dwyer and Stewart, 1986a) (Figure 5.7, Equation 2.3). Only the parameter for the area of the largest leaf was affected by fertiliser P (Figure 5.7, Table 5.2). This demonstrates that it was only the extent to which the leaves expanded that was affected by P levels and not their relative distribution. None of the coefficients X_0, c or d were altered by the P fertiliser treatment (Table 5.2), whereas Y_0 (the area of the largest leaf) was markedly reduced when no P was applied. The data reviewed in Section 2.3.1.2 were consistent with this, and show that changes in crop leaf area were associated with changes in Y_0 and not changes in the other curve coefficients.

Conceptually these individual leaf areas can be explained using a similar procedure to the effect of N in maize (Section 2.3.1.2). Based on the results of Muchow (1988a), Sinclair and Muchow (1995) indicated that individual leaf area was adjusted to maintain a minimum canopy SLN of 0.55 g N m^{-2}. Such a relationship may also have occurred here with leaf area being adjusted to maintain a minimum concentration of P in leaves. These leaf P concentrations will be examined in further Chapter 6.

5.4.4 FSA and GLAI

FSA was minor in these crops and did not exceed 0.3 for any treatment (Figure 5.10). Consequently calculated GLAI did not decrease markedly later in crop development (Figure 5.11). This lack of major leaf senescence meant that the curves of calculated RI_{cum} did not have an obvious asymptote (Figure 5.13). Similarly, in 'Challenger' sweet corn grown previously at Lincoln, values of FSA were less than 0.1 for fully irrigated treatments (Stone *et al.*, 2001b). Leaf senescence had only a minor effect on GLAI in sweet corn, with the major effects coming from the area of individual leaves and their temporal pattern of appearance. If crops had been allowed to achieve physiological maturity as in grain maize, then FSA would have been of greater importance in determining GLAI and hence a plateau level of RI_{cum} would have been apparent. The study of Stone *et al.* (1999) illustrates this in grain maize. The FSA reached 1.0 (i.e. all leaves had senesced) and therefore GLAI decreased to a value of 0 before harvest, therefore there was a clear plateau of RI_{cum}.

Major leaf senescence became apparent after 821°Cd and 472 °Cd in 2001/02 and 2002/03 respectively (Figure 5.10). The latter value is consistent with previous literature where FSA increased after 440°Cd in 'Challenger' sweet corn (Stone *et al.*, 2001b) and 400 °Cd in maize (Birch, 2003). This supports the idea that the onset of leaf senescence is genetically controlled beginning approximately 400-450 °Cd after emergence (Borras *et al.*, 2003). The 821°Cd found in 2001/02 was probably caused by the uncoupling of temperature data between the microclimate of the site and Broadfields' meteorological station, as for phenological development (Section 4.4.5.1). Moreover the position and slope of the second line segment in 2001/02 relies heavily on three points from each treatment. If a more extensive range of data were available then it is likely that the break point found in the two line segments would have

been earlier. This is supported by the greater slope of the second line segment in 2001/02 compared with 2002/03 (Figure 5.10). However, this more rapid increase in FSA may have been associated with the late water stress in Experiment 1 (Figure 3.2), as demonstrated by Stone *et al.*, (2001b).

P fertiliser did not change the dynamics of leaf senescence in 'Challenger' sweet corn (Figure 5.10). This was consistent with previous research (Colomb *et al.*, 2000; Plenet *et al.*, 2000b) where there were only minor and ambiguous effects of P fertiliser on maize leaf senescence (Section 2.3.1.3). Furthermore, FSA differences in these maize experiments were only apparent after canning maturity would have occurred in sweet corn.

This contrasts with the effect of N deficiency which accelerates leaf senescence in maize crops (Muchow, 1988a). Both N and P can be re-mobilised in maturing plants (Morris *et al.*, 1985). The lack of a P effect on senescence was probably due to the overriding importance of N remobilisation. The sink strength of the developing grains for N was greater than the sink strength for P, so that a P limitation did not alter leaf senescence but an N deficiency did.

5.5 Conclusions

- 'Challenger' sweet corn supplied with P fertiliser accumulated more intercepted solar radiation than crops receiving no P fertiliser.
- Accumulated intercepted of solar radiation was greater (RI_{cum} increased by ~ 200 MJ m^{-2} when 200 or 240 kg P ha^{-1} was applied compared with crops that received no P fertiliser) in crops receiving P fertiliser due to both a faster rate of leaf appearance (phyllochrons for leaf tip appearance decreased by ~5°Cd when P was applied compared with the 0 kg P ha^{-1} crops) and an increased size of individual leaves (Y_0 increased by 80-160 cm^2 when 200 or 240 kg P ha^{-1} was applied compared with the 0 kg P ha^{-1} crops).
- The extinction coefficient was 0.65 and did not differ between P treatments.
- Leaf senescence was minor (FSA<0.3) and unaffected by P supply for any of the treatments.

Chapter 6. Radiation use efficiency and photosynthesis of 'Challenger' sweet corn in response to fertiliser P.

6.1 Introduction

Chapter 5 showed that applying P fertiliser to 'Challenger' sweet corn increased crop total RI_{cum}. This partly explains the increased sweet corn yield with fertiliser P reported in Chapter 4. However, total yield also requires consideration of RUE (Equation 1.1), which may also have been affected by P fertiliser.

Environmental factors that increase leaf photosynthesis usually also increase RUE (Section 2.3.2.1). For example, N fertiliser has been shown to increase maize leaf photosynthesis and hence RUE (Section 2.3.2.2), both of which are closely related to SLN (Muchow and Davis, 1988; Muchow and Sinclair, 1994). In contrast reported RUE responses to fertiliser P are ambiguous (Section 2.3.2.2), although photosynthesis has been shown to be reduced in young P deficient maize plants grown in controlled environments (Section 2.3.3.3).

In this chapter the relationship between RI_{cum} (calculated in Chapter 6) and the total above ground crop DM of sweet corn crops is analysed for the duration of the crop (Section 3.7.3). Consequently responses of RUE to fertiliser P are examined. As an explanatory variable, leaf photosynthesis was measured on individual leaves using an infrared gas analysis (IRGA) system, which is related to leaf N and P concentrations. RUE and photosynthesis are closely related to temperature (Sections 2.3.2.1 and 2.3.3.2). Therefore an RUE temperature response function for maize (Wilson *et al.*, 1995) is also examined for sweet corn.

6.2 Materials and methods

6.2.1 Radiation use efficiency

Initially crop RUE was taken as the slope of a linear regression of above ground crop DM (g DM m^{-2}) (Section 3.7.3) against RI_{cum} (MJ solar radiation m^{-2}) for the crop duration from emergence to final harvest. RI_{cum} was calculated using the method in Chapter 5 (Figure 5.13). Initially regressions were made for individual plots in both Experiment 1 and 4. These regressions were forced through the origin (0, 0) based on the fact that a crop that has accumulated 0 MJ m^{-2} of RI_{cum} has a biomass of 0 g DM m^{-2}. RUE of individual P treatments were then tested using ANOVA (Section 3.8).

This first analysis indicated no significant treatment effects of P on RUE. Therefore the subsequent analysis used the pooled data set for treatments and seasons. RUE was then determined using a linear model with two segments. A similar method was used to that outlined in Section 5.2.3. In this regression analysis the number of fully expanded leaves for each treatment at a given harvest date was used to partition the data to each line segment. The critical number of fully expanded leaves was moved sequentially in one leaf intervals. The maximum R^2 was used as a basis to select the critical number of fully expanded leaves.

6.2.2 Leaf photosynthesis

6.2.2.1 Photosynthetic rate

Leaf photosynthesis rates were measured using the LI-6400 portable photosynthesis system (Licor Inc., Lincoln, NE, USA) on individual leaves from selected plots on five dates (Table 6.1) in each of Experiments 1 and 4 (Sections 3.3 and 3.4). This instrument uses an IRGA to compute net photosynthesis of a single leaf clamped into a 6 cm^2 chamber as the difference between the CO_2 concentration at the leaf surface and at a reference IRGA.

The LI-6400 allows complete control over light, temperature and ambient CO_2 concentration in the chamber. Measurements were taken from the youngest fully expanded leaf, when photosynthetic rates were at a maximum (Section 2.3.3.2), from plants in selected plots at solar noon ± 2 hours on clear cloudless days (incident solar radiation 17-33 MJ m^{-2} day^{-1}).

Photosynthetic light response curves consisting of seven levels of PPFD (2000, 1000, 750, 500, 250, 100, and 0 μmol m^{-2} s^{-1}) were measured on each selected plant using the 'Auto light curve' program with a minimum wait time of 90 seconds and a 3% coefficient of variation as the trigger to move to the next PPFD setting. The maximum wait time used was 120 seconds. These curves started at 2000 μmol m^{-2} s^{-1}PPFD and finished at 0 μmol m^{-2} s^{-1}, because this allowed the most rapid stabilisation of photosynthesis at each PPFD level. Standard conditions of 400 μmol CO_2 m^{-2} and 25 °C were used in the leaf chamber. This was close to the optimum temperature for maize leaf photosynthesis of 27 °C (Section 2.3.3.2) and represents a typical summer maximum temperature in Canterbury.

Due to time constraints in stabilizing the instrument between individual measurements only one leaf was sampled per plot. These time constraints also meant that it was impossible to sample each plot on a given date; therefore P treatments were chosen to measure the range in P supply. Thus on some dates the 0, 100/110 and 200/240 kg P ha^{-1} plots were sampled in all three replicates, while on other dates all five P treatments were sampled from only two replicates. In some instances conditions during measurement became unsuitable to continue and these data sets were incomplete. Incomplete data sets were included in subsequent regression analyses to give 80 complete light curves. These 80 light curves consisted of 45 from Experiment 1 (2001/02) and 35 from Experiment 3 (2002/03). Of these 24 curves were

from the 0 kg P ha^{-1} plots, 5 from the 50 kg P ha^{-1} plots, 24 from the 100/110 kg P ha^{-1} plots, 5 from the 150/170 kg P ha^{-1} plots, and 22 from the 200/240 kg P ha^{-1} plots.

Table 6.1 Sample dates for measuring leaf photosynthesis using the LI-6400 in Experiments 1 and 4.

2001/02 (Experiment 1)	2002/03 (Experiment 3)
18 January 2002	27 December 2002
2 February 2002	29 December 2002
9 February 2002	15 January 2003
23 February 2002	16 January 2003
25 February 2002	17 February 2003

In 2001/02 light curves were measured on crops with >8 leaves. However, P had a greater effect on the photosynthesis of lower leaves (Section 6.3.2). Therefore in 2002/03 samples were taken from plants with 5-16 leaves. Leaves < 5 were not sampled because of their small area (Figure 5.7, Section 5.3.1.5) and mass, leading to errors in determining P and N concentrations and hence SLP and SLN (Section 6.2.2.2), and also sampling difficulties with leaves close to the ground.

6.2.2.2 Specific leaf area, P and N concentration of leaves

After the measurement of each light curve, the leaf lamina was detached at the point of attachment with the leaf sheath and its position (labelled acropetally, Section 3.7.1.1) noted. The area of each leaf was determined using a Licor 3100 area meter (Licor Inc, Lincoln, NE, USA). The leaves were then dried in a fan-forced oven and weighed. Leaf area and DM measurements were used to calculate the specific leaf area (SLA; $cm^2\ g^{-1}$) for each individual

leaf. These leaves were then ground to 0.5 microns using a Cyclotec 1093 sample mill (Foss, Sweden) and the concentrations of P and N were determined using method 4B of Blakemore *et. al.* (1987). The concentration of P and N ($g\ g^{-1}$) and the SLA ($m^2\ g^{-1}$) were used to calculate SLP ($g\ P\ m^{-2}$) and SLN ($g\ N\ m^{-2}$) respectively for each leaf.

6.2.2.3 Statistical analysis

Non- rectangular hyperbolae were fitted to Photosynthetic rates at each PPFD level (Section 2.3.3.1) using least squares regression for each leaf measured with θ constrained to be >0.3.

From these curves the rate of photosynthesis at 2000 $\mu mol\ m^{-2}\ s^{-1}$ PPFD was calculated (P_{2000}). P_{2000} was regarded as an appropriate level of PPFD for comparing photosynthetic rates amongst treatments because it equates to the maximum expected on a clear cloudless day in Canterbury (Section 2.3.3.1).

The relationship between SLP and SLN of individual leaves was examined using least squares regression.

The relationships between P_{2000}, α or Rd (dark respiration) with SLP for each leaf were examined using least squares regression analyses. The relationship between SLP and P_{2000} was examined using an asymptotic relationship in the form of Equation 4.1. However, in this instance A and B were constrained to be identical so that the regression passed through the origin. The relationships between SLP and α or R_d were examined using a linear function.

6.3 Results

6.3.1 Radiation use efficiency

There was no effect of fertiliser P on RUE in either 2001/02 or 2002/03 (Appendix 12). Therefore mean data points were pooled for treatments and both seasons. A two step linear regression was then fitted to the combined data set (Section 6.2.1) using the number of fully expanded leaves to select the data on each line segment. This showed that there was a change in RUE when there were ~ 10 fully expanded leaves. RUE was 0.66 g DM MJ^{-1} when there were <10 fully expanded leaves and 1.34 g DM MJ^{-1} when there were ≥10 fully expanded leaves (Figure 6.1).

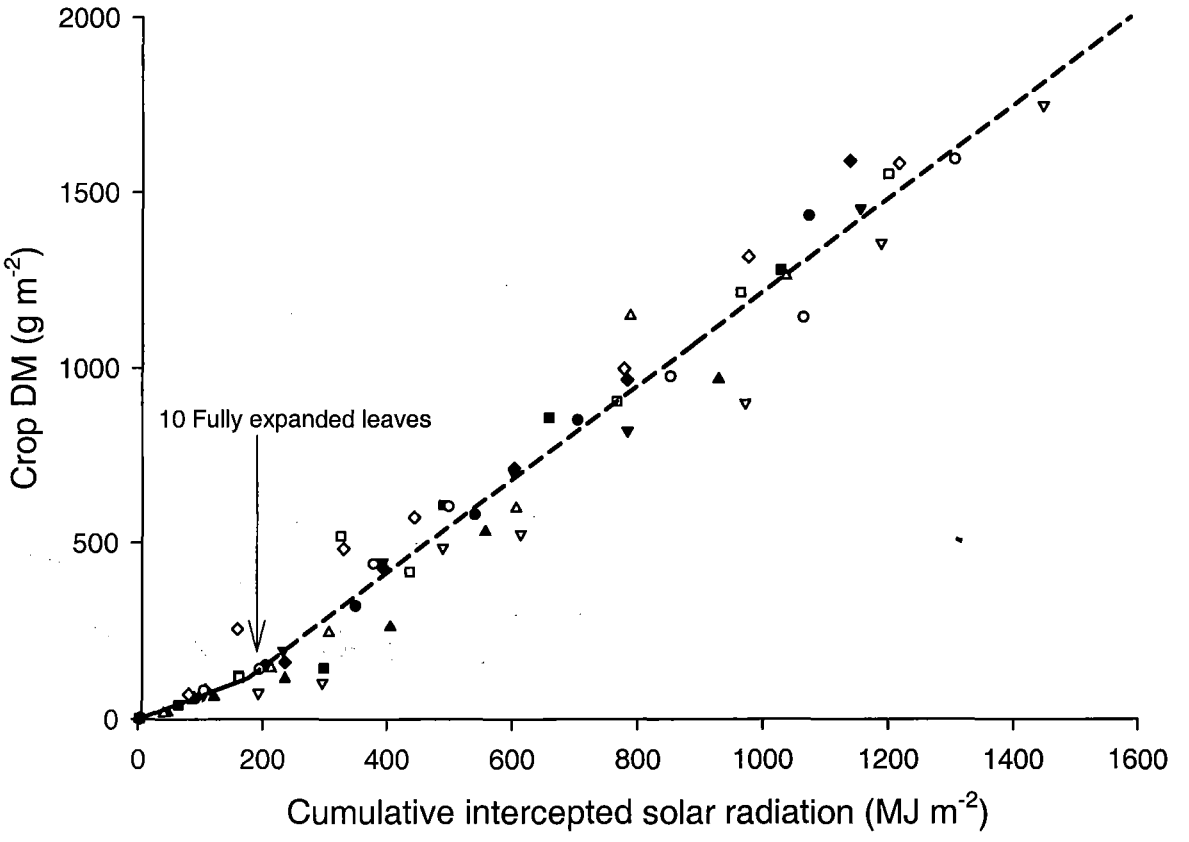

Figure 6.1 Relationship between cumulative intercepted solar radiation (MJ m^{-2}) and above ground crop dry matter (g m^{-2}) for 'Challenger' sweet corn grown at Lincoln, Canterbury, New Zealand at five rates of fertiliser P in 2001/02 and 2002/03. (Symbols in Table 4.1). The fitted model is y=0.66 x (Fully expanded leaf number < 10; solid regression line), y =1.34 x –120 (Fully expanded leaf number ≥ 10; Dashed regression line); R^2 = 0.97.

6.3.2 Photosynthesis, P and N content of leaves

There was a strong linear relationship (R^2 > 0.82) between SLP and SLN (Figure 6.2). For every 0.1 g P m^{-2} increase in SLP the SLN increased by 0.8 g N m^{-2}. However, residual analysis indicated a systematic error. When SLP was < 0.1 g P m^{-2} the SLN fell off more rapidly than would be expected from the complete linear regression (dotted line, Figure 6.2). The overall range in SLN was 0.53 to 2.98 g N m^{-2} leaf, with the corresponding range in SLP

from 0.034 to 0.30 g P m^{-2} leaf. The greatest SLP found in a 0 kg P ha^{-1} treatment was 0.193 g P m^{-2} for leaf 15 on 23 February 2002.

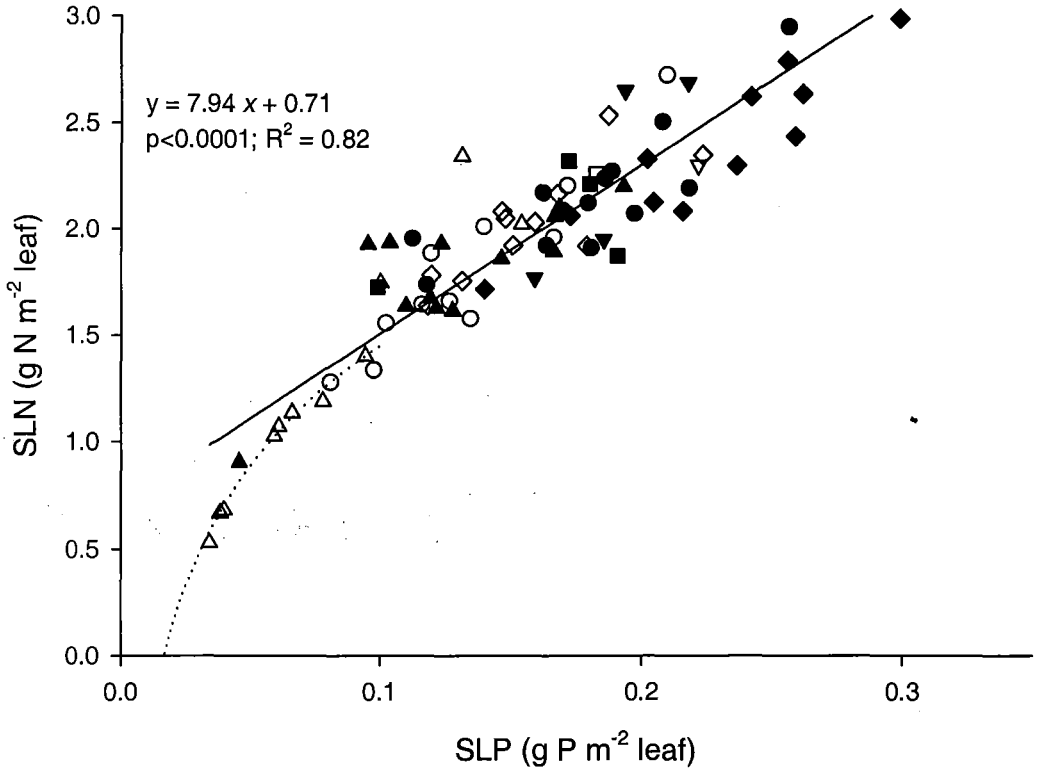

Figure 6.2 Relationship between specific leaf phosphorus (SLP) and specific leaf nitrogen (SLN) in leaves of 'Challenger' sweet corn grown at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03 at a range of P fertiliser rates. (Symbols in Table 4.1). The solid line represents the linear regression, while the dotted line represents a logarithmic relationship for SLP values <0.1 g P m^{-2} leaf.

The non-rectangular hyperbolae described the photosynthetic light response curve data (R^2> 0.99). Figure 6.3 shows a representative photosynthetic light response curve for a plot receiving 100 kg P ha^{-1}, measured on 15 January 2003. The fitted values of θ were low

(θ<0.8) in 70 out of 80 light curves, and hence curves were generally not light saturated at 2000 μmol PPFD m^{-2} s^{-1}.

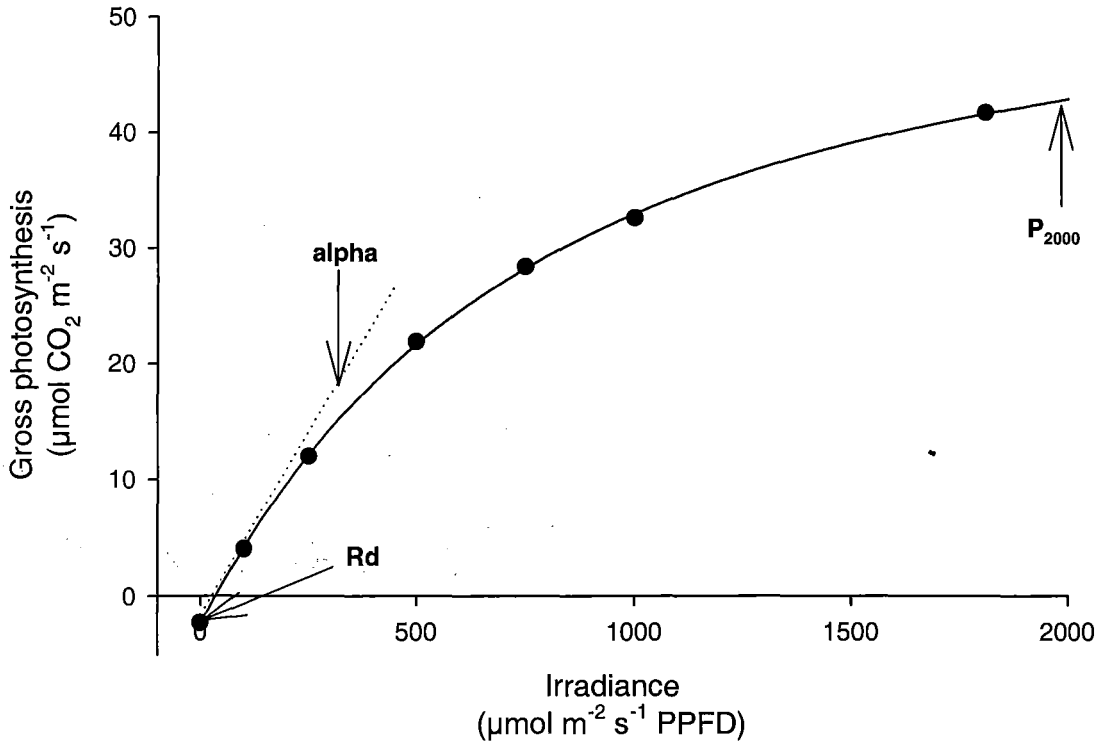

Figure 6.3 Representative photosynthetic light responsive curve measured with the LI-6400, for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand. This measurement was taken from leaf 8 (numbered acropetally) on 15 January 2003 from a crop that had received a total of 110 kg P ha^{-1} over two seasons. The three major variables used for further analyses are labelled, Rd (Rate of dark respiration; μmol CO_2 m^{-2} s^{-1}), α (initial slope of the hyperbola; μmol CO_2 μmol $PPFD^{-1}$), and P_{2000} (Rate of gross photosynthesis at 2000 PPFD; μmol CO_2 m^{-2} s^{-1}).

There was a weak asymptotic (R^2= 0.29) relationship between P_{2000} and SLP with the asymptote at 38.7 (±3.1) μmol CO_2 m^{-2} s^{-1} and a steep decline in P_{2000} when SLP was <0.1 g P m^{-2} (Figure 6.4).

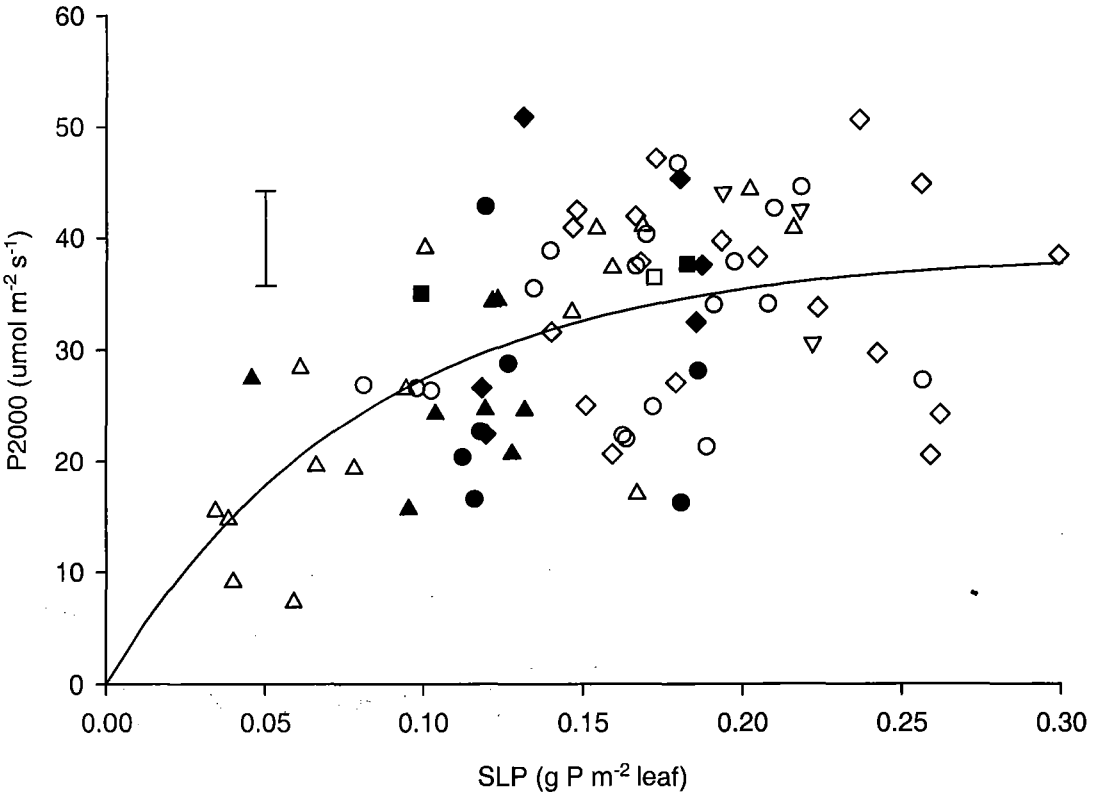

Figure 6.4 Relationship between specific leaf phosphorus (SLP; g P m^{-2} leaf) and rate of leaf photosynthesis at 2000 µmol m^{-2} s^{-1} PPFD (P_{2000}; µmol CO_2 m^{-2} s^{-1}) for all leaves, measured using the LI 6400, for 'Challenger' sweet corn grown in 2001/02 and 2002/03 at Lincoln, Canterbury, New Zealand. (Symbols in Table 4.1) The fitted relationship is y=38.7-38.7[±3.1](0.0000043 [±0.000013] ^{x}); R^2=0.29. The error bar represents the estimated standard error of the observations.

The decrease in P_{2000} when SLP was <0.1 g P m^{-2} was due principally to the early leaves (≤11, but especially 5-7) on plants that did not receive P fertiliser (Figure 6.5). For leaves ≥12 the range of SLP was always on the upper part of the curve (>0.1 g Pm^{-2}) and therefore P_{2000} was consistent among treatments (Figure 6.5c and d). However, for leaves 5-7, plants that did not receive any P fertiliser had SLP <0.1 g P m^{-2} and P_{2000} was < ~20 µmol CO_2 m^{-2} s^{-1}. In

contrast, plants that received P fertiliser had SLP of ≥0.1 g P m^{-2} and P_{2000} was 20-40 μmol CO_2 m^{-2} s^{-1} (Figure 6.5a).

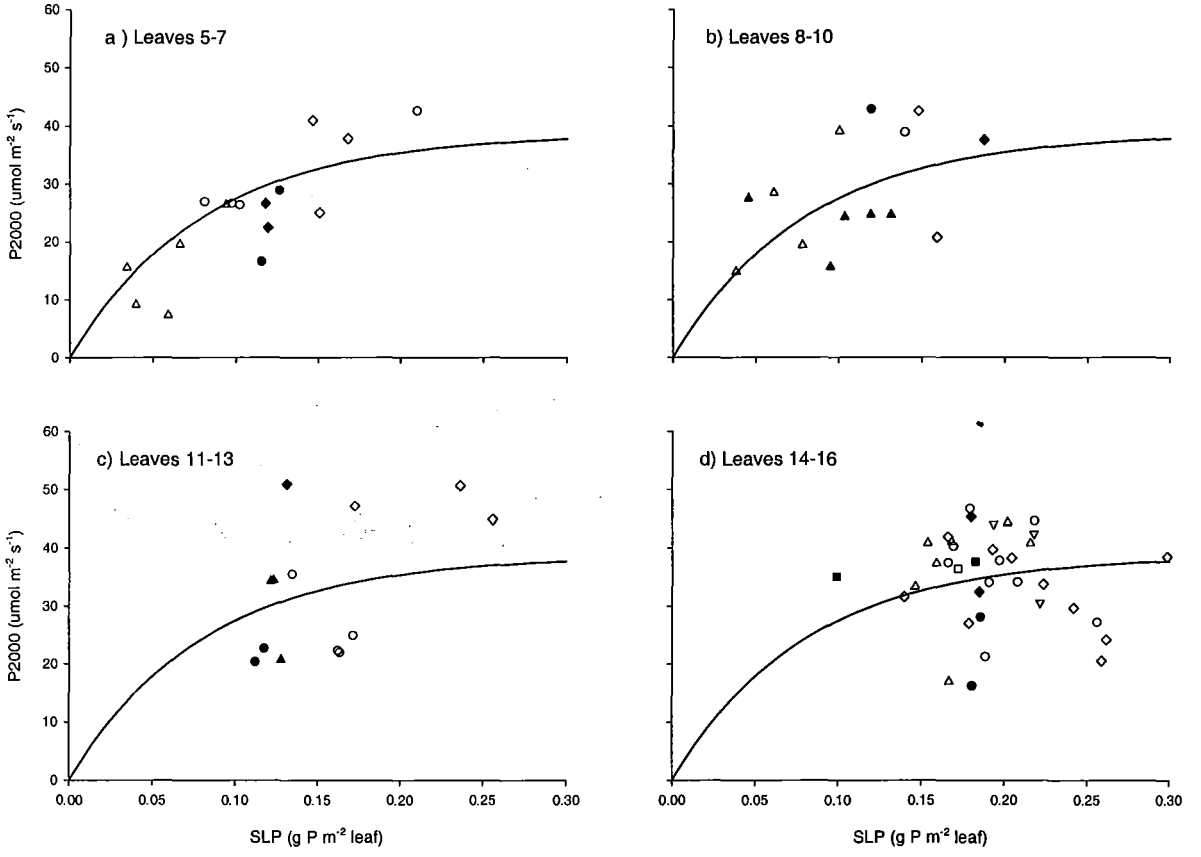

Figure 6.5 Relationship between specific leaf phosphorus (SLP; g P m^{-2} leaf) and rate of leaf photosynthesis at 2000 μmol m^{-2} s^{-1} PPFD (P2000; μmol CO_2 m^{-2} s^{-1}) for leaves 5-7 (a), 8-10 (b), 11-13 (c) and 14-16 (d) measured using the LI -6400, for 'Challenger' sweet corn grown in 2001/02 and 2002/03 at Lincoln, Canterbury, New Zealand. (Symbols in Table 4.1). The fitted relationship is as for Figure 6.4.

There was no effect of SLP on R_d or α with the mean R_d being 3.2 (±0.14) μmol CO_2 m^{-2} s^{-1} (Figure 6.6a) with the mean α being 0.069 (±0.002) μmol CO_2 μmol $PPFD^{-1}$ (Figure 6.6b).

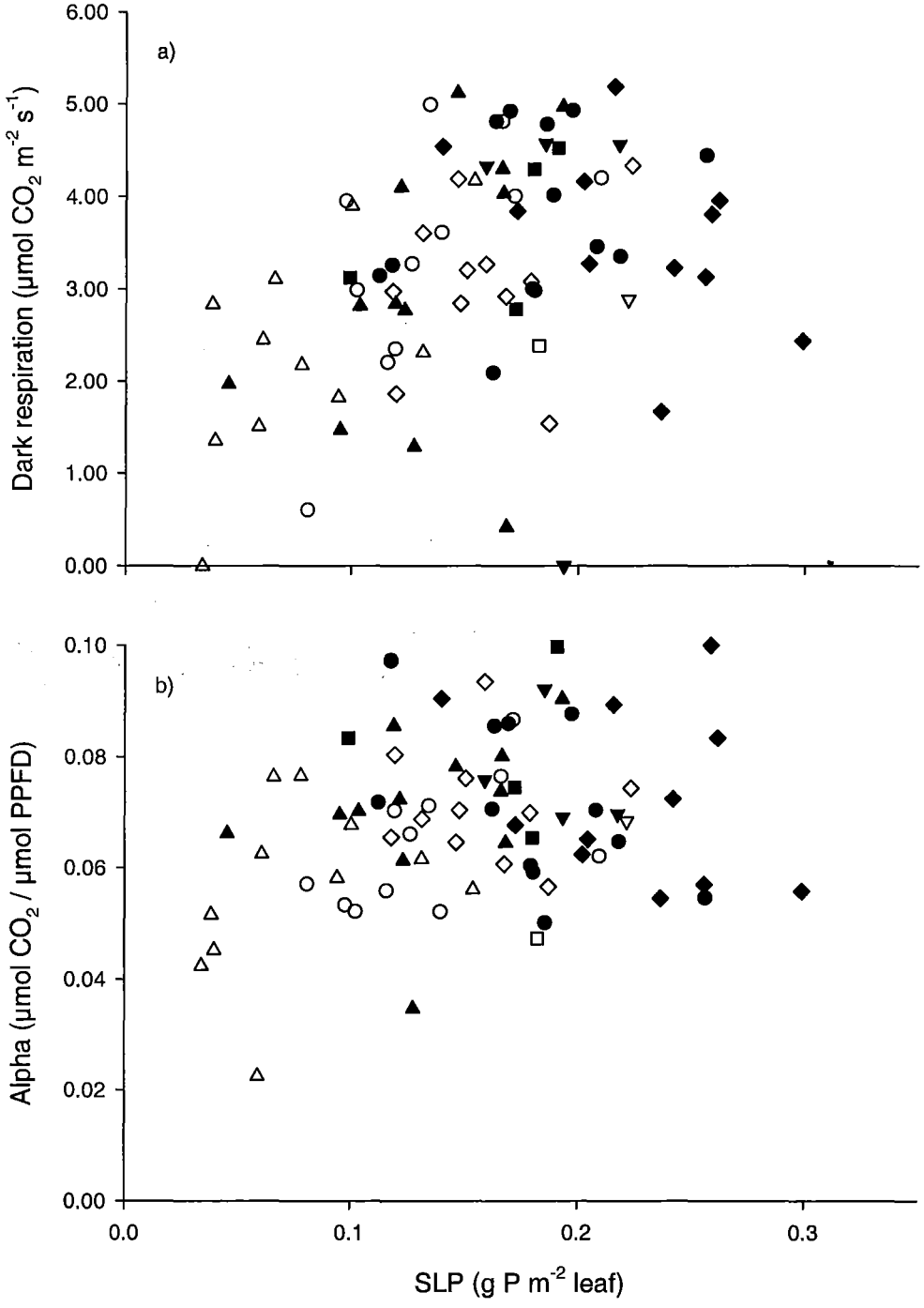

Figure 6.6 Relationship between specific leaf phosphorus (g P m^{-2}) and dark respiration (µmol CO_2 m^{-2} s^{-1}) (a) and α (µmol CO_2 µmol $PPFD^{-1}$) (b) of 'Challenger' sweet corn leaves grown at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03 at a range of P fertiliser levels. Values of Rd and α were determined using a LI-6400. Symbols are outlined in Table 4.1.

6.4 Discussion

6.4.1 RUE

The consistent RUE across the range of P treatments used (Figure 6.1) suggests the increases in total crop DM (9.7-15.9 t DM ha^{-1}), and hence kernel yield (Chapter 4) associated with increasing P fertiliser were caused by changes in RI_{cum} (Section 5.3.4.2) rather than the efficiency of use of intercepted solar radiation. These results were consistent with those of Plenet *et al.* (2000a) who showed maize RUE was unaffected by fertiliser P, but contrast with those of Colomb *et al.* (1995) with sunflower and Rodriguez *et al.* (2000) with wheat who showed that applied P increased crop RUE. The implication is that a RUE response to P may be species-specific.

The lack of an RUE response to P (Figure 6.1) was also inconsistent with the general maize response to limited N supply where both RUE and RI_{cum} decreased (Muchow, 1994; Muchow and Davis, 1988; Muchow and Sinclair, 1994). This indicates a fundamental difference in the action of P and N stress on *Zea mays* crops. With the exception of leaf positions <8, SLPs in these sweet corn crops were >0.1 g P m^{-2}. However, changes in SLP between 0.1 and 0.3 g P m^{-2} did not affect leaf photosynthetic rates (Figure 6.5) and hence crop RUE was stable (Figure 6.1).

RUE was lower during crop establishment than during the major part of growth (Figure 6.1). When the number of fully expanded leaves was < 10 RUE was only 0.66 g DM MJ^{-1}, but when the number of fully expanded leaves was ≥10 then RUE was 1.34 g DM MJ^{-1}. This was consistent with previous experiments in a range of crops (Section 2.3.2.1). For example, Giauffret *et al.* (1991) found maize RUE of 0.44 g DM MJ^{-1} in the early crop stages and then 1.35 g DM MJ^{-1} until silking. Similarly, Trapani *et al.* (1992) showed sunflower RUE was

0.55 g DM MJ^{-1} during establishment (0-47 days after sowing) and then 1.2 g DM MJ^{-1} until anthesis.

A potential explanation of the low RUE early in the season was that mean air temperatures were less during spring than summer (Table 3.2) and hence RUE was lower. However, using calculated RI_{cum} (Section 5.3.4.2), the temperature response function for RUE from Wilson *et al.* (1995) and daily mean temperatures resulted in an over prediction of total crop DM when there were less than 10 fully expanded leaves (Figure 6.7). Measured crop DM was only 0.49 (±0.04) of that predicted when there were less than 10 fully expanded leaves (solid line). When there were more than10 fully expanded leaves the slope of the relationship between actual crop DM and predicted crop DM was 1 (± 0.04) (see dotted line in Figure 6.7). Thus, the temperature response function for maize RUE of Wilson *et al.* (1995) was appropriate for the majority of sweet corn growth but it did not account for the low RUE early in the season.

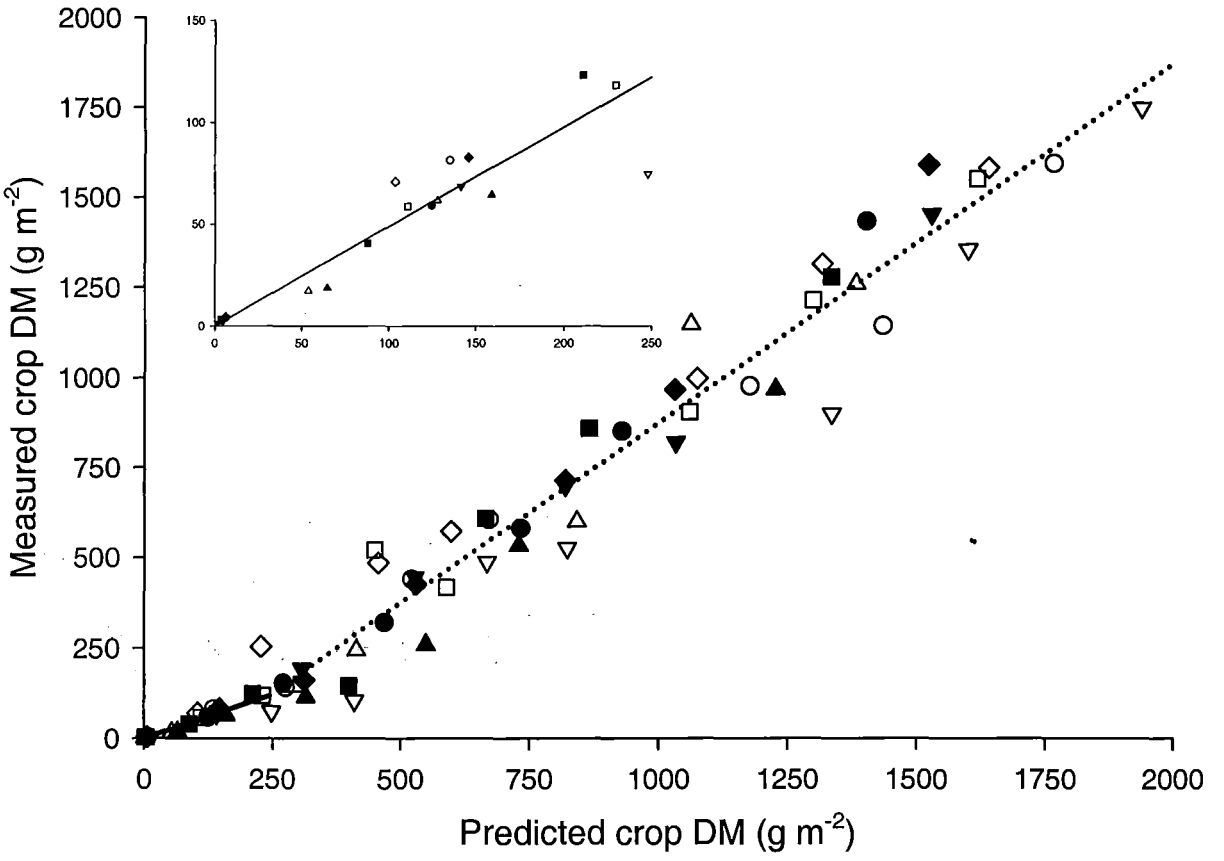

Figure 6.7 Comparison of predicted crop dry matter (g m^{-2}) using RI_{cum} (Figure 5.13), the temperature response for RUE of Wilson *et al.* (1995) (i.e. If T_{mean}>16°C, RUE = 1.6 g DM MJ^{-1}; If T_{mean} <8°C RUE = 0 g DM MJ^{-1}; If 8 °C <Tmean> 16 °C, RUE= (T_{mean}-8 °C)*0.2 g DM MJ^{-1}) and daily mean temperature measured at Broadfields' meteorological station, with actual crop dry matter (g m^{-2}) for 'Challenger' sweet corn grown with five rates of fertiliser P in 2001/02 and 2002/03 (Symbols and treatments as in Table 4.1) at Lincoln Canterbury, New Zealand. The solid line (y = 0.49 (±0.04) x) is for crops with < 10 fully expanded leaves and the dotted line (y = -124.6 (± 38.4) + 1 (±0.04) x) is for crops with ≥10 fully expanded leaves. The inset figure is for predicted DM less than 250 g m^{-2} and is provided for clarity.

The low RUE during crop establishment may also have been caused by earlier leaves having a lower potential photosynthetic capacity (Section 2.3.2.1). However this hypothesis was not supported by the data in Figure 6.4 that showed when P was not limiting P_{2000} was similar for all leaves. Alternatively during crop establishment the low GLAI may have meant leaves were light saturated and hence RUE was lower. This also seems unlikely, as the leaves were generally not light saturated at 2000 μ mol PPFD m^{-2} s^{-1} (Figure 6.3). Light saturation at low GLAI would be more likely in a C3 than this C4 crop. Increased partitioning to the roots during establishment may also have decreased apparent RUE. In the study of Tollenaar (1989b), partitioning of DM to roots was 1.4 times greater during the 4 to 8 leaf stage than during the 8 to 12 leaf stage. This may have contributed to the lower RUE but does not fully account for the ~ 2 fold difference (Figure 6.4). Furthermore, sunflower RUE was still lower during establishment when root growth was accounted for (Trapani *et al.*, 1992).

Regardless of the mechanism responsible the data have shown two different RUEs in 'Challenger' sweet corn. This change in RUE would be of greatest consequence for sweet corn crops grown in a cool temperate climate such as Canterbury, because crop development would be slower than in warmer or tropical regions. This may also explain why this effect has not been more widely reported previously for maize. Experiments have generally been in tropical or sub-tropical locations where crop development is rapid and hence a change in RUE that occurred early in crop growth (10 fully expanded leaves) may not have been obvious or important. In addition to the current experiments in a temperate climate (43° 62' S), which have shown this low RUE during crop establishment, the studies of Giauffret *et al.* (1991) and Plenet *et al.* (2000a) have also indicated this effect in France.

6.4.2 Comparison of RUE with previous studies

The RUE found in the current study was 1.30 g DM MJ^{-1} for the major part of 'Challenger' sweet corn growth. This was consistent with similar studies with maize in New Zealand (Section 2.3.2) where RUE ranged from 1.2-1.4 g DM MJ^{-1}, but is less than the 1.6-1.7 g DM MJ^{-1} commonly regarded as the upper limit for maize RUE in an optimal environment (Kiniry *et al.*, 1989; Sinclair and Muchow, 1999). In the current study and the two previous examples from New Zealand (Stone *et al.*, 1998c; Stone *et al.*, 1999), temperature would have limited RUE. The data in Figure 6.7 shows that the temperature response function of Wilson *et al.* (1995) can account for this, with the exception of the low RUE when there were <10 fully expanded leaves.

The current data are also inconsistent with the experiment of Stone *et al.* (2001a), where 'Challenger' sweet corn was grown at Lincoln and had a maximum RUE of ~1.75 g DM MJ^{-1}. The mean air temperature during this experiment measured at the Broadfields' meteorological station was 14.4 °C. Using the temperature response function of Wilson *et al.* (1995) an RUE of 1.28 g DM MJ^{-1} would better explain the crop DM data. Therefore it seems that the value of RUE found by Stone *et al.* (2001a) may have been overestimated. This could have occurred due to the use of an assumed extinction coefficient of 0.4 when calculating RI_{cum}. In the current study k = 0.65 was measured. By using a lower value of k when GLAI was ≤ 3, it is likely that Stone *et al.* (2001a) under-estimated RI_{cum} (Section 5.4.2) and hence overestimated RUE. In the current analysis, assuming k = 0.4 the calculated RUE would have been 0.91 g DM MJ^{-1} when RI_{cum} <81 MJ m^{-2} and 1.7 g DM MJ^{-1} when $RI_{cum} \geq 81$ MJ m^{-2}. The latter value is similar to the RUE reported by Stone *et al.* (2001a) and highlights the potential impact of an overestimated RUE in their study.

6.4.3 Photosynthesis

The asymptotic relationship between SLP and leaf photosynthetic rate (Figure 6.4) was expected based on previous controlled environment results (Jacob and Lawlor, 1991; Payne *et al.*, 1996). The low R^2 (0.29) showed that factors other than P nutrition had a major impact on photosynthesis. It is possible that day-to-day and plot-to-plot variation in: leaf age and position (Dwyer and Stewart, 1986b; Stirling *et al.*, 1994), air temperature (Tollenaar, 1989a; Tollenaar *et al.*, 1991), chilling damage (Long *et al.*, 1983; Stirling *et al.*, 1993; Ying *et al.*, 2002), solar radiation environment (Ward and Woolhouse, 1986), water status and vapour pressure were probably also having a major impact on leaf photosynthesis. This highlights the importance of confirming field responses of photosynthesis to P, rather than using controlled environment studies (Section 2.3.3.3). Furthermore, it was only in the early leaves (<8) that P_{2000} was reduced by the lack of P fertiliser (Figure 6.5). This shows a limitation of controlled environment studies where predominantly young plants that may not produce more than 8-10 leaves are sampled (Section 2.3.3.3). Clearly such results can be misleading when extrapolated to predict the impact on crop yield for the duration of growth for an entire season.

In an attempt to quantify the other environmental effects on leaf photosynthesis a regression was established between P_{2000}, measured in the 200/240 kg P ha^{-1} crops, and each of the daily records of vapour pressure deficit, midday air temperature (when measurements were obtained), minimum air temperature of the previous night (chilling damage), and daily incoming solar radiation, for each of the eight days on which measurements were taken (Table 6.1). These regressions were then used to estimate a theoretical maximum of P_{2000} for each measurement date (Table 6.1), and the relative value of P_{2000} (i.e. P_{2000}/ maximum P_{2000}) for individual treatments of all plots were then plotted against SLP. This method did not increase

the R^2 (R^2< 0.36) of the relationship and indicates that there were other unexplained factors influencing P_{2000}.

Closer relationships between leaf P concentration and photosynthetic rate than that found here have been obtained in growth chamber experiments (e.g. Usuda and Shimogawara, 1991). There are few examples of relationships between P_{max} and SLP, but a previous relationship between P_{max} and SLN in a cotton crop (Milroy and Bange, 2003) had a similarly poor fit (R^2 = 0.48, n = 598). In contrast, Muchow and Sinclair (1994) found much better relationships between SLN and P_{max} (R^2>0.90) in sorghum and maize. However, their R^2 were obtained using a method where photosynthesis data were divided into SLN ranges of 0.2 g N m^{-2} and the median P_{max} from each group was used in the regression. This procedure assumed that factors other than SLN were limiting photosynthesis and the median value represented the true response to SLN. When this method was applied to the P_{2000} data in this experiment, by breaking the data into SLP groups of 0.025 g P m^{-2} the R^2 was 0.70, but the regression equation was identical (Figure 6.4). The validity of using such an approach is questionable.

The range of SLPs for the different leaves (Figure 7.2) explains the lack of P effect on RUE (Figure 6.1). In the early leaves (<8) lack of P fertiliser reduced P_{2000} as a consequence of having SLP <0.1 g P m^{-2} leaf, (Figure 6.5a). The primary role of these lower leaves is to establish the subsequent crop canopy. This explains the lower GLAI and the delay in establishment of GLAI as a result of a delayed leaf appearance and the reduced individual leaf area (Section 5.3.2) in crops receiving no P. These plants could not maintain SLP of leaves <8 above 0.1 g P m^{-2} and were thus slower to establish a canopy.

In contrast, in leaves >8, SLP was always >0.1 g P m^{-2} (Figure 6.5b-d) for all treatments and hence P_{2000} was consistent across P treatments. These later leaves were larger than the earlier leaves (Section 5.3.1.5) and consequently had a dominant effect in determining GLAI and RI_{cum} for the major part of the crop growth cycle. Once a sufficient number of leaves (>8) had been established there were only negligible changes in photosynthesis, and hence RUE was consistent across treatments. The growth rate when these larger leaves were present dominated responses over a season. Therefore calculated seasonal RUE did not differ between P fertiliser treatments (Figure 6.1). This also potentially explains why Plenet *et al.* (2000a) found no change in RUE of field grown maize when P supply was limiting growth, but Mollier and Pellerin (1999) found an indication of a lower RUE in P deficient young maize plants (11-27 days after germination) in a greenhouse experiment.

There was variation in both Rd and α, and this was not related to the SLP of individual leaves (Figure 6.1). Consequently these two parameters had no impact in determining RUE. This is consistent with the results of Rodriguez *et al.* (1998b) who showed that the leaf P concentrations of wheat had no effect on either Rd or α, but had a major impact on P_{max}.

6.4.4 Leaf P and N concentration

The strong linear relationship between the SLP of an individual leaf and SLN (Figure 6.2) was consistent with Belanger and Richards (1999) where N supply was limited in timothy (*Phleum pratense*). The fact that SLN increased at a rate ~8 times greater than SLP is consistent with the data reviewed by Jones (1983) that showed maize shoot N:P ratios are mostly between 5 and 10. The greater accumulation of N compared with P is most likely due to the requirement for large amounts of N in plant proteins such as Rubisco. The link between P and N status of leaves suggests that photosynthesis and RUE responses to P fertiliser may be mediated through their effects on the N status of leaves. Whatever the case the link allows

direct comparison between experiments where maize RUE and photosynthesis have been measured in relation to SLN.

The minimum SLN found in the current study was 0.53 g N m^{-2} leaf (Figure 6.2). This was similar to the minimum of 0.55 g N m^{-2} found by Muchow (1988b) and used by Sinclair and Muchow (1995) to modify leaf area development in their model of maize response to N supply. In the current study there was a consistent trend in the plants that did not receive P fertiliser for SLP and hence SLN to fall as successively lower leaves were sampled. It is likely that if even lower leaves (<5) had been sampled then SLN may have decreased further. This can not be substantiated, but is based on the observation that sweet corn seedlings with 2-3 leaves that received 0 kg P ha^{-1} fertiliser were pale yellow (Plate 6), a common symptom of N deficiency.

Plate 6 Experiment 3 on 5 January 2003. The red lines outline the approximate borders of the plots. The plot in the foreground received 240 kg P ha^{-1}, and the plot in the background received 0 kg P ha^{-1}.

There was a clear deviation in the relationship between SLP and SLN when SLP fell below 0.1 g P m^{-2} leaf. This was also approximately when further decreases in SLP had a marked effect on P_{2000} (Figure 6.4). This value of 0.1 g P m^{-2} is equivalent to a SLN of 1.5 g N m^{-2} leaf. Using this value of SLN maize RUE would be predicted to be ~1.7 g DM MJ^{-1} (Muchow and Davis, 1988), which is maximal for maize crops (Kiniry *et al.*, 1989; Sinclair and Muchow, 1999). Both the leaf photosynthesis and canopy RUE values of Muchow and Sinclair (1994) decreased with SLNs <1.5 g N m^{-2}. This consistency provides confidence in proposing 0.1 g P m^{-2} or 1.5 g N m^{-2} as a threshold level for both RUE and photosynthesis in maize and sweet corn. Decreases in SLP or SLN below these will result in decreased assimilate production per unit of intercepted solar radiation and, if they occur early in crop growth, have ongoing effects on crop yield.

6.5 Conclusions

- 'Challenger' sweet corn crop RUE was 0.66 g DM MJ^{-1} during establishment (<10 fully expanded leaves) and 1.34 g DM MJ^{-1} subsequently, but was unaffected by P supply. Therefore changes in crop biomass (Chapter 4) were attributable solely to changes in RI_{cum} (Chapter 5).
- With the exception of the establishment phase, RUE values for all crops were consistent with those expected from the temperature response function proposed by Wilson *et al.* (1995) where RUE is reduced when mean daily air temperatures fall below 16°C.
- Generally leaf photosynthesis was unaffected by P, explaining the conservative RUE response. An exception was the photosynthetic rate of leaves <8 which were reduced when SLP fell below a threshold level of ~0.1 g P m^{-2} leaf. These leaves determined the size of the subsequent canopy, but were only minor determinants of sweet corn growth during its major period.

Chapter 7. Simulating long term 'Challenger' sweet corn yield and phenology in response to P supply.

7.1 Introduction

In Chapter 4 kernel yields of 'Challenger' sweet corn showed a positive asymptotic response to P fertiliser. However, this response was site and season specific (Section 2.2), due to seasonal differences in incident solar radiation and temperature. Expanding the application of these results to other environments and seasons requires collection of long term fertiliser-yield response records from multiple sites. Alternatively, a more efficient method may be the simulation of kernel yield response to P fertiliser using an appropriate crop model and long-term weather records. From these analyses long-term probability distributions of yield can be calculated (e.g. Muchow and Bellamy, 1991).

In this chapter a cultivar specific crop simulation model is developed and tested to simulate long-term yields of 'Challenger' sweet corn at both Lincoln and Hastings. This model is based on the structure developed by Muchow *et al.* (1990) (Figure 2.9) and assumes that water is non-limiting. As a first step key growth and development variables (Chapter 5 and Chapter 6) are related to soil P (Appendix 2). These relationships are then incorporated in the model, which is tested against previously published data. This test does not include variation in P supply. Therefore a second test of the simulated responses to P (Experiments 1 and 4) is included.

Long-term weather data sets are then used to simulate kernel yields for a range of soil P levels at both Lincoln and Hastings in New Zealand. In Canterbury delaying sowing past 15 October increases the risk of sweet corn crops failing to mature before the first autumn frost (Wilson and Salinger, 1994). It is expected that the delayed maturity with limited P (Section 4.3.4) is

also likely to increase this risk. Therefore the long term probability of 'Challenger' sweet corn failing to mature is also quantified with respect to P supply at both Lincoln and Hastings.

7.2 Materials and methods

7.2.1 Model structure

The model was based on the framework of Muchow *et al.* (1990) (Figure 2.9) and included some modifications for a cool temperate climate (Wilson *et al.*, 1995).

As a first step five crop variables were related to available soil P (Appendix 2). These were the phyllochron (Section 5.3.1.1), the curvature parameter (b) of the relationship between Tt and the number of fully expanded leaves (Section 5.3.1.3), the area of the largest leaf (Y_0; Section 5.3.1.5), the Tt (Tb = 8°C) between emergence and silking (Section 4.3.4.2) and the Tt (Tb = 0°C) between silking and maturity (Section 4.3.4.2). The relationship between these measured variables and available soil P (Olsen P), as measured for each crop at the end of each experimental season, was examined using least squares regression. It is recognised that the soil P could have been obtained before each crop was sown. However, this would also include errors because of the timing of the fertiliser applications close to the sowing date of each crop. It is unlikely that the Olsen P of each crop decreased substantially over the time period of each experiment (~160 days). The relationships of phyllochron and Tt from emergence to silking with Olsen P were examined using a 3-parameter exponential decay curve (Equation 7.1 a). The relationships of b, Y_0 and Tt from silking to maturity with Olsen P were examined using a 3-parameter exponential rise to maximum curve (Equation 7.1 b).

$$y = a + b\exp^{(-cxOlsenP)}$$

Equation 7.1 a

Where y = response variable; a = asymptotic value of y; a+b= value of y when Olsen P = 0 μg ml^{-1}; and c = curvature of the relationship.

$$y = a + b(1 - \exp^{(c \times OlsenP)})$$

Equation 7.1 b

Where y = response variable; a+b = asymptotic value of y; a = value of y when Olsen P = 0 μg ml^{-1}; and c = curvature of the relationship.

These relationships were calculated using Olsen P based on the fact that this gave a representation of soil available P that was not dependant on fertiliser P. A mechanistic model of P uptake based on various pools of P in the soil and the interrelationships between them and the environment (e.g. Probert, 2004) would be more appropriate. However, this would require a detailed knowledge of the P dynamics in this soil. However, these were not collected in these experiments. Therefore, the relationships in Equation 7.1 a and b are specific to the soil and environmental conditions in Experiments 1 and 4. However, they are better than simple relationships with applied P fertiliser.

7.2.2 Model framework

These relationships were then integrated into the model framework. The model works on a daily time step and is based on the linear relationship between intercepted solar radiation and crop DM (RUE). The input variables were Olsen P, sowing date, plant population and daily weather data. The daily weather data required are minimum and maximum air temperatures (°C) and incident solar radiation (MJ m^{-2}).

Accumulated Tt is calculated using the method described in Section 4.2.2.4 (i.e. Tb = 8 °C and Tt is calculated for eight intervals of three hours and integrated for each day). If the crop

has emerged i.e. Tt >65°Cd (Section 4.3.4.1) daily GLAI is constructed using the method outlined in Section 2.3.1.4. In this construction it was assumed that the variables for a (Equation 5.1), X_0, c and d (Equation 2.3), and the final number of leaves (Section 5.2.1.4) were constant (Table 7.1) and not affected by P supply.

It was assumed that plant population did not affect any of the variables relating to GLAI development. This is a simplification, given that plant population can affect both the area of individual leaves (Maddonni *et al.*, 2001a), leaf appearance rates (Bos *et al.*, 2000a) and canopy senescence (Borras *et al.*, 2003) in maize. However, within the plant populations examined here and the comparatively low GLAI's the effects of inter-plant competition would be minimal. Furthermore this model analysis ignores the effect of both temperature and light on these aspects of GLAI (Bos *et al.*, 2000b; Stone *et al.*, 1999).

The phyllochron (Section 5.2.1.1), b (Section 5.2.1.3) and Y_0 (Equation 2.3) are assumed to change with Olsen P using the responses established above. The equation for predicting FSA was taken from Experiment 3 (2002/03) (i.e. FSA was $4.0*10^{-5}$ * Tt when Tt<478°Cd and $3.8*10^{-4}$ *Tt - 0.16 when Tt>478°Cd, (Figure 5.10b)) as this was based on the larger data set and was therefore expected to be more reliable than the 2001/02 response.

Table 7.1 Input variables into the 'Challenger' sweet corn crop model that were held constant for simulations.

Parameter	Description	Value
Tt sowing - emergence	(Section 4.3.4.1)	65°Cd
a	Y- intercept of fully expanded leaves in relation to Tt (Figure 5.4)	2.1 leaves
X_0	Position of largest leaf (Figure 5.7)	11.5
c	Breadth of individual leaf area / leaf position curve (Figure 5.7)	0.0545
d	Skewness of individual leaf area / leaf position curve (Figure 5.7)	$2.15*10^{-4}$
Final number of leaves	(Figure 5.6)	17.5 leaves

Daily RI was calculated from GLAI by assuming that k =0.65 (Figure 5.12). Daily growth was then calculated by multiplying daily RI by RUE and this was accumulated until crop maturity. RUE was calculated from the temperature response function of Wilson *et al.* (1995) and mean daily temperature (Equation 7.2). When there were < 10 fully expanded leaves RUE was set at half of the temperature limited maximum (Section 6.4.1; Figure 6.7).

If $T_{mean} \geq 16$ °C $\quad$ RUE = 1.6 g MJ^{-1}

If $T_{mean} \leq 8$ °C $\quad$ RUE = 0 g MJ^{-1}

If 16 °C < T_{mean} > 0 °C $\quad$ RUE = 0.2 g MJ^{-1} × Tmean - 1.6 g MJ^{-1}

Equation 7.2

Where T_{mean} = mean daily temperature (°C).

Accumulated Tt from emergence to silking (Tb = 8°C) and silking to maturity (Tb = 0°C) was taken from the relationship with Olsen P. These two values were used in conjunction with daily maximum and minimum air temperatures to predict the date of harvest maturity. A HI of 0.24 was used at maturity to predict kernel yield from crop biomass (Section 4.3.2).

7.2.3 Model testing

Two tests were performed to establish the accuracy of this framework for simulated vs observed yields. In both cases simulated and observed values were compared using residual mean squared deviations (RMSD) (Equation 7.3).

$$RMSD = \sqrt{\left(\frac{\sum (\text{Observed} - \text{Predicted})^2}{\text{Number of observations}} \right)}$$

Equation 7.3

7.2.3.1 Test 1. Independent data

In the first test the model framework was tested against data from three experiments in which 'Challenger' sweet corn had been grown in New Zealand and for which the key management

inputs were known (Table 7.2). In these tests the harvest date was taken as that used in each treatment. In the water deficit study (Stone *et al.*, 2001a) only the fully irrigated crops were examined. In the experiments with multiple cultivars (Rogers *et al.*, 2000; Stone *et al.*, 2004) only the data for 'Challenger' were examined. In these experiments it was assumed that P did not limit growth, based on the high fertility levels of these experiments and the addition of substantial P fertiliser (Table 7.2). On this basis all variables were set at their asymptotic value.

Table 7.2 Crop cultural details of 'Challenger' sweet corn crops used to test the model. The specific details of each experiment were kindly provided by P.J. Stone.

Reference	Location	Sowing Date	Plants ha^{-1}	Olsen P $\mu g\ ml^{-1}$	Fertiliser P (kg ha^{-1})	Harvest date
(Rogers *et al.*, 2000)	Hastings	21 Sep 1999	59500	26	30	23 Jan
		28 Sep 1999	59500	26	30	26 Jan
		11 Oct 1999	59500	26	30	4 Feb
		27 Oct 1999	59500	26	30	8 Feb
		9 Nov 1999	59500	26	30	21 Feb
		23 Nov 1999	59500	26	30	1 Mar
		8 Dec 1999	59500	26	30	13 Mar
		21 Dec 1999	59500	26	30	8 Apr
		6 Jan 2000	59500	26	30	18 Apr
		20 Jan 2000	59500	26	30	2 May
(Stone *et al.*, 2004)	Hastings	25 Oct 2000	66700	28	30	26 Feb
		1 Dec 2000	66700	28	30	18 Mar
(Stone *et al.*, 2001a)	Lincoln	30 Oct 1996	57000	17	20	22 Mar

7.2.3.2 Test 2. P response from Experiments 1 and 4

The ability of the model to predict biomass and kernel yield responses of 'Challenger' sweet corn to P supply (Experiments 1 and 4) was tested using Olsen P (Appendix 2) as an input parameter. It is recognised that the output of this test is confounded based on the fact that the model variables and the model testing were taken from the same crops. In the absence of an extensive data set a more rigorous test of the simulations was not possible.

In this test the silking and harvest dates were also compared with observed dates (corrected for kernel moisture content; Section 4.2.2.4) using RMSD (Equation 7.3).

7.2.4 Long-term simulations

The model was then used to simulate long-term kernel yield trends at both Hastings (39° 47' S, 176° 64' E) and Lincoln (43° 62'S, 172° 44'E). At Lincoln long-term weather data was from 1960-2003. But due to incomplete data sets 1973-1976 and 1994 were excluded, giving 38 complete seasons. At Hastings the long-term weather data was from 1976-2002, with 25 complete seasons. Long term mean air temperatures from November to March were ~2 °C warmer at Hastings than at Lincoln and mean solar radiation receipts were similar (Table 7.3).

Table 7.3 Mean daily air temperatures (°C) and mean daily incoming solar radiation (MJ m^{-2}) at Lincoln (1960-2003) and Hastings (1976-2002) for November to March.

Month	*Mean daily air temperature (°C)*			*Mean daily incoming solar radiation (MJ m^{-2})*		
	Lincoln	Hastings	Difference	Lincoln	Hastings	Difference
November	13.1	15.0	+1.9	21.0	20.8	-0.2
December	15.2	17.4	+2.2	22.7	21.9	-0.8
January	16.6	18.5	+1.9	22.1	21.9	-0.2
February	16.4	18.3	+1.9	16.2	18.8	+2.6
March	14.8	16.7	+1.9	14.1	15.3	+1.2

Simulations were made for four theoretical crops sown with Olsen P = 6, 10, 20 or 30 μg ml^{-1} on two dates (31 October, and 30 November) at both sites for each season. These sowing dates were chosen because they represent the limits of the approximate sowing window in Canterbury. A single population of 60 000 plants ha^{-1} was used. Frosts occurring before harvest maturity were assumed not to kill the crop. The long-term simulated kernel yields for each sowing date, location and P supply combination were analysed using probability of exceedance (e.g. Robertson *et al.*, 2003).

A second set of long-term simulations at both Lincoln and Hastings and using the same four Olsen P levels were made to investigate the risks associated with crops failing to mature before the first killing autumn frost. If a simulated crop did not reach canning maturity before the first killing autumn frost or before 30 April it was deemed to have failed. A killing frost

was defined as a minimum air temperature < –1°C or grass minimum < –3°C (Wilson and Salinger, 1994). Simulations were run for nine sowing dates, beginning 15 October and then at 10-day intervals until 3 January for each season. The long-term probability that each P supply and sowing date combination would fail to reach canning maturity for each site was calculated (Wilson and Salinger, 1994).

7.3 Results

7.3.1 Relationships of crop growth and development variables with soil P values

The phyllochron decreased exponentially (R^2=0.76) with increasing soil Olsen P from ~35°Cd with 6 = μg P ml^{-1} to an asymptotic value of 26.3 °Cd with >30 μg P ml^{-1} (Figure 7.1a). There were strong exponential increases in both b (R^2=0.64) and Y_0 (R^2=0.54) with increasing soil Olsen P. The asymptotic value of b was 0.0038 (Figure 7.1b), and the asymptotic value of Y_0 was 543 cm^2 (Figure 7.1c).

Similarly there were strong asymptotic relationships between soil Olsen P and both Tt (Tb = 8°C) from emergence to silking (R^2=0.80) and Tt (Tb = 0 °C) from silking to emergence (R^2 = 0.93). The Tt between emergence and silking decreased exponentially from 720°C with Olsen P = 6 μg ml^{-1} to the asymptotic value of 572°Cd when Olsen P > 30 μg ml^{-1} (Figure 7.2a). The Tt from silking to maturity increased from 760°Cd with Olsen P = 6 μg ml^{-1} to its asymptotic value of 898 °Cd when Olsen P > 30 μg ml^{-1} (Figure 7.2b).

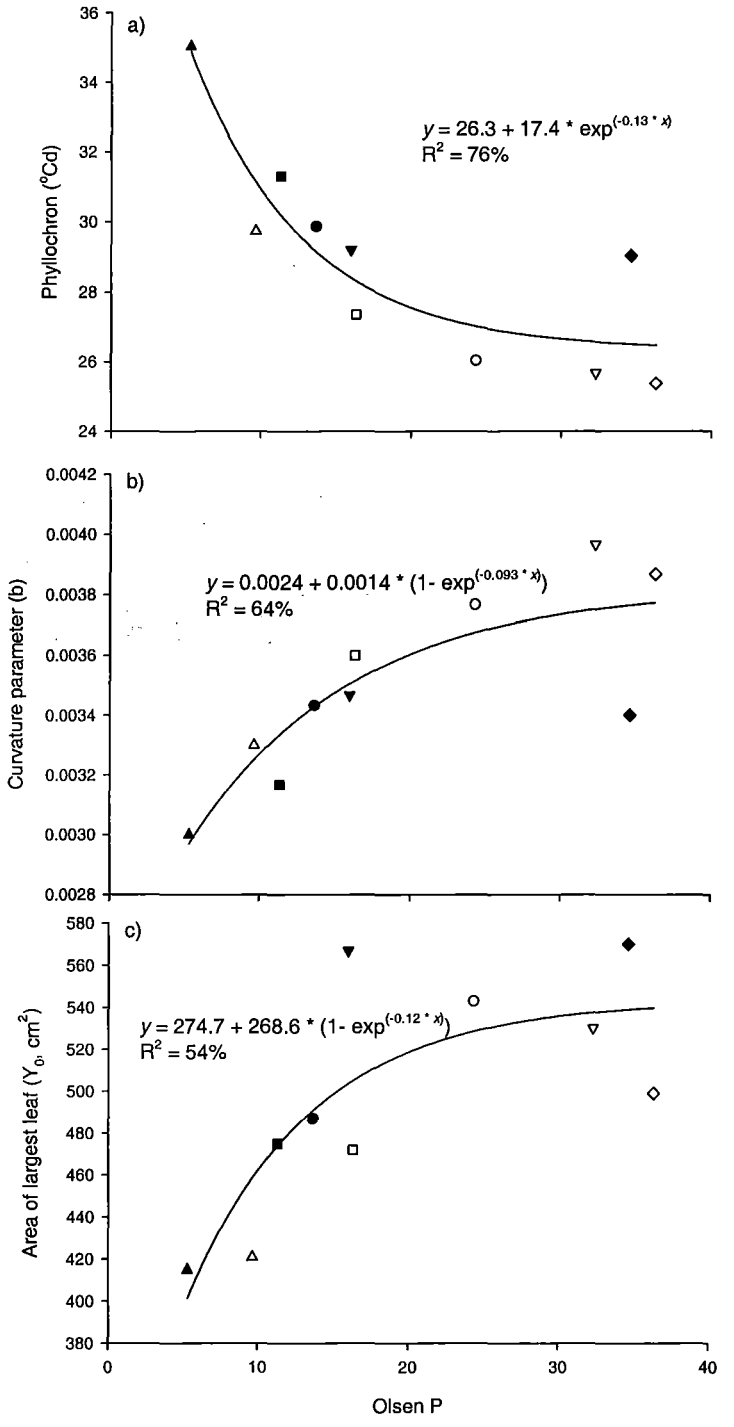

Figure 7.1 Relationships of measured phyllochron (°Cd) (a), dimensionless curvature parameter between fully expanded leaf appearance and Tt (b), and area of the largest leaf (Y_0; cm^2) (c) with soil Olsen P ($\mu g\ ml^{-1}$) for 'Challenger' sweet corn grown in Experiments 1 and 4. (Symbols in Table 4.1).

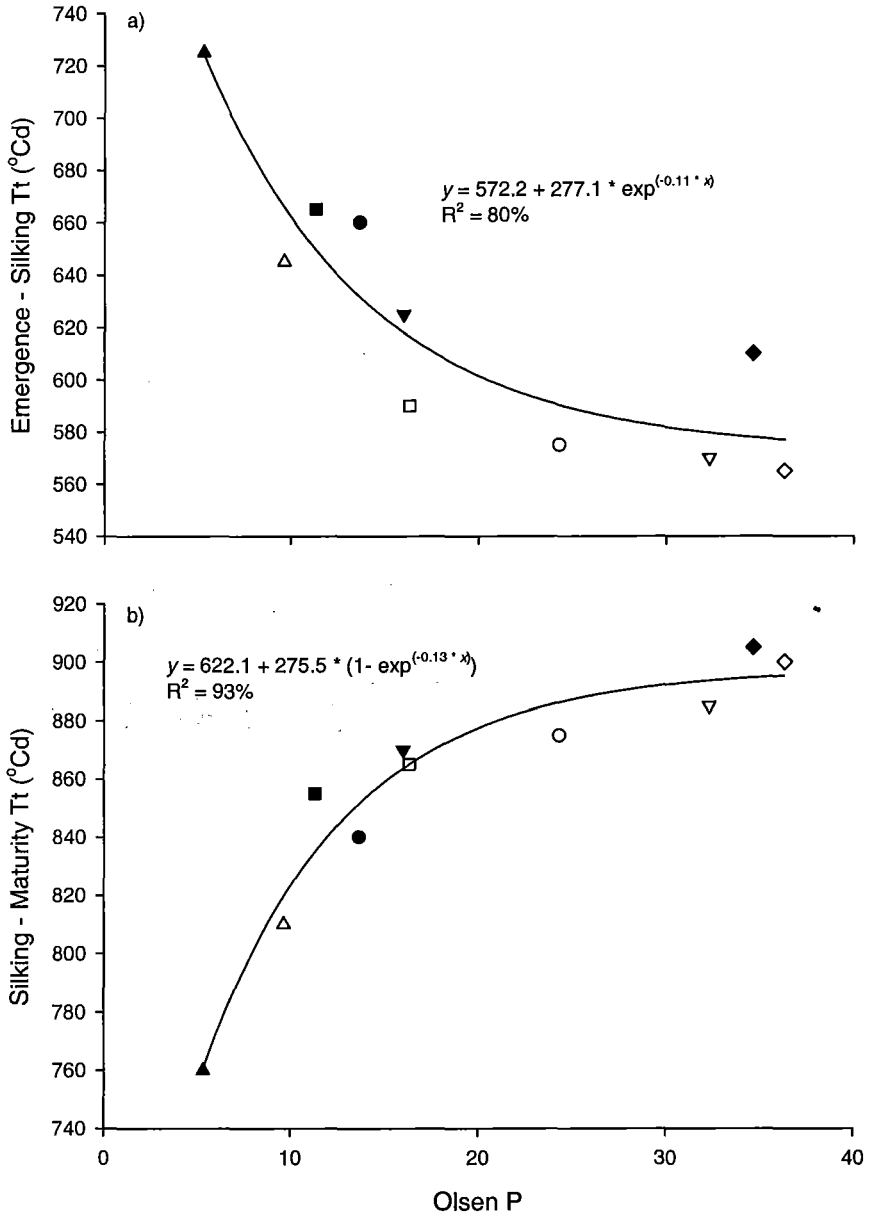

Figure 7.2 Relationships of measured Tt (Tb = 8°C) from emergence to silking (°Cd) (a), and Tt (Tb= 0°C) from silking to canning maturity (b) with soil Olsen P (µg ml^{-1}) for 'Challenger' sweet corn grown in Experiments 1 and 4. (Symbols in Table 4.1).

7.3.2 Model testing and refinement

7.3.2.1 Test 1

The model outlined in Section 7.2.1 under predicted both the kernel yield and crop biomass (Figure 7.3). The RMSD was 1.35 t ha^{-1} for kernel DM yield or 33% of average observed yield, and 3.42 t ha^{-1} for crop biomass or 23% of average observed yield. There was less variation in simulated crop biomass indicating that a single HI was inappropriate for the crops tested. The raw data (Table 7.2) indicated a range in HI for the sweet corn crops tested ranging from 0.21 to 0.37. Furthermore, the regression lines in Figure 7.3 showed that the neither the trends in kernel yield or crop biomass were well predicted by the model.

The most likely cause for the under prediction of crop biomass and kernel yields was an under estimate of the area of the largest leaf (cm^2) (Y_0). Variation in Y_0 for a given genotype of maize has been shown previously in diverse but non-limiting environments. For example Y_0 for the hybrid Dekalb XL82 have ranged from ~600 cm^2 in Katherine (14° S 28' S, 132° 18' E) Australia (Muchow and Carberry, 1989) to ~850 cm^2 in Gatton (27° 33' S, 152° 20' E), Australia (Birch *et al.*, 1998b). Both experiments applied irrigation and nutrients at non-limiting rates. Changes in Y_0 such as these may possibly be caused by differences in plant population or air temperature. However, in Experiments 1 and 4 maximum Y_0 was ~550 cm^2 for 'Challenger' sweet corn grown at Lincoln, but the data of Stone *et al.*, (2001b) indicated that Y_0 for 'Challenger' was ~750 cm^2 also grown at Lincoln at an almost identical plant population. The reason for these changes in the area of individual leaves is unclear.

Therefore a sensitivity analysis was performed on the independent data set (Table 7.2) comparing the RMSD and both the slope and intercept of a regression between simulated and measured crop yields by systematically increasing Y_0 from 550 cm^2 to 1100 cm^2 in 50 cm^2

increments. This analysis showed that Y_0 = 900 cm^2 gave the best fit to the data set (Figure 7.4; RMSD = 1.64 t ha^{-1}). However, this is illogical as the maximum reported Y_0's for 'Challenger' in the literature are <800 cm^2. Furthermore, using the consistent relationship between final leaf number and Y_0 of Keating and Wafula (1992) there would be an estimated Y_0 of 840 cm^2 in a maize hybrid with 17.3 leaves. There was only a minor increase in crop biomass RMSD when Y_0 = 800 cm^2 (RMSD = 1.78 t ha^{-1}) was used compared with Y_0 = 900 cm^2 (RMSD = 1.64 t ha^{-1}) (Figure 7.5). This variation is similar to previously reported literature values for maize crop biomass (e.g. RMSD = 1.79 t ha^{-1}, Wilson *et al.* 1995). Therefore in the long-term yield simulations (Section 7.3.3.1), the asymptotic value of Y_0 was set to 800 cm^2, and decreased proportionately by Olsen P to the previously found relationship (Figure 7.1c).

The slope and intercept of the regression between observed and predicted crop biomass both decreased as Y_0 increased (Figure 7.4b and c). With Y_0 = 800 cm^2 the slope was 1.62 and the intercept was -8.09 for crop biomass. This indicates that although the RMSD (1.64 t ha^{-1}) was acceptable for crop biomass, the model was somewhat limited in predicting the trends of crop biomass yield. This indicates that the model should not be used to simulate yields in environments where simulated crop biomass is <10 t DM ha^{-1} or >18 t ha^{-1} (Figure 7.5).

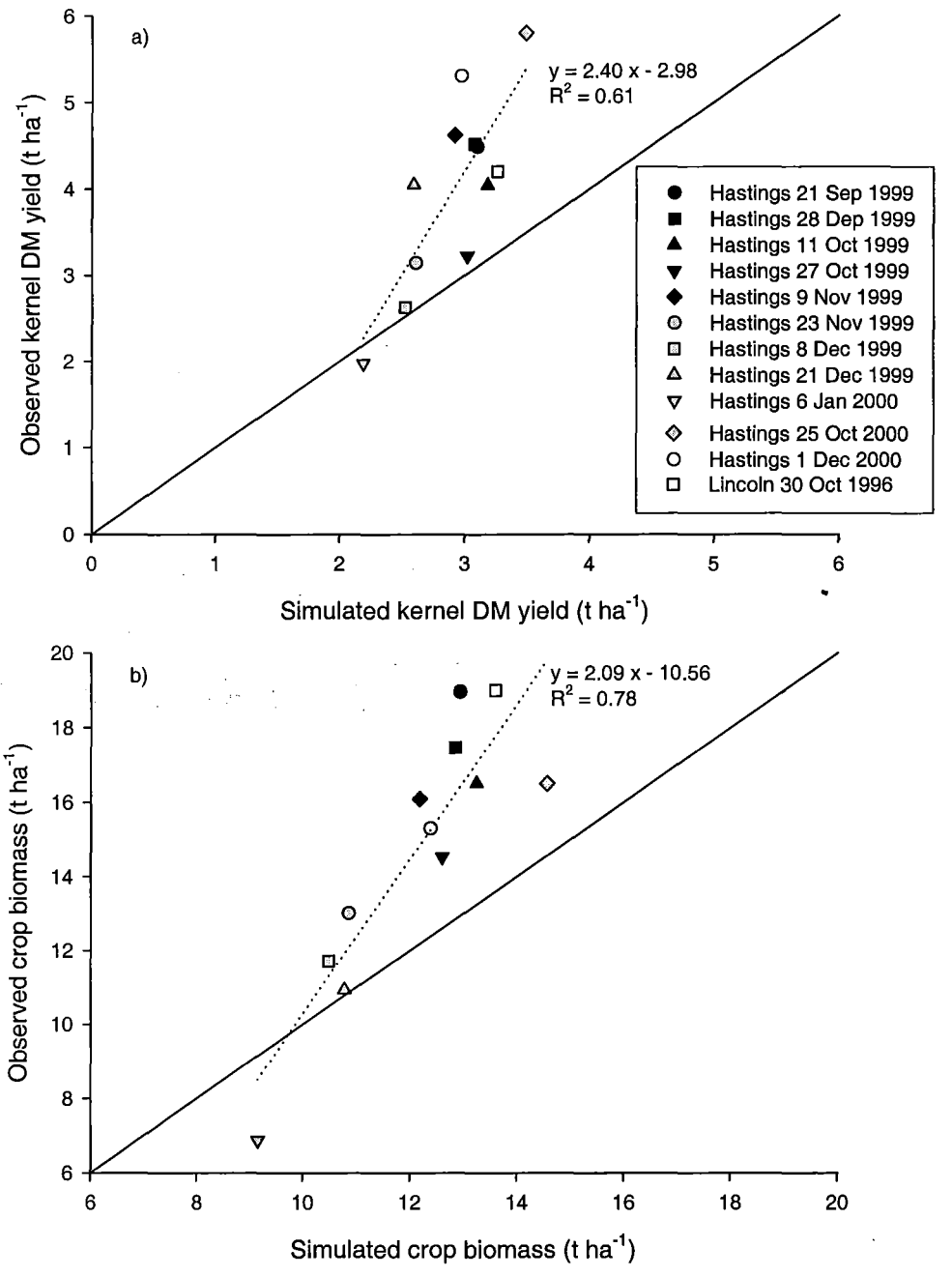

Figure 7.3 Comparison of simulated and observed values of kernel DM yield (t ha^{-1}) (a), and total crop DM (t ha^{-1}) (b), for 'Challenger' sweet corn grown in the experiments outlined in Table 7.2. The simulated values were obtained using the model outlined in Section 7.2.1. RMSD's were 1.35 t ha^{-1} in (a) and 3.42 t ha^{-1} in (b). The dotted lines are least squares linear regressions and the solid lines are 1:1 lines. Sowing dates, locations and symbols are outlined in the legend.

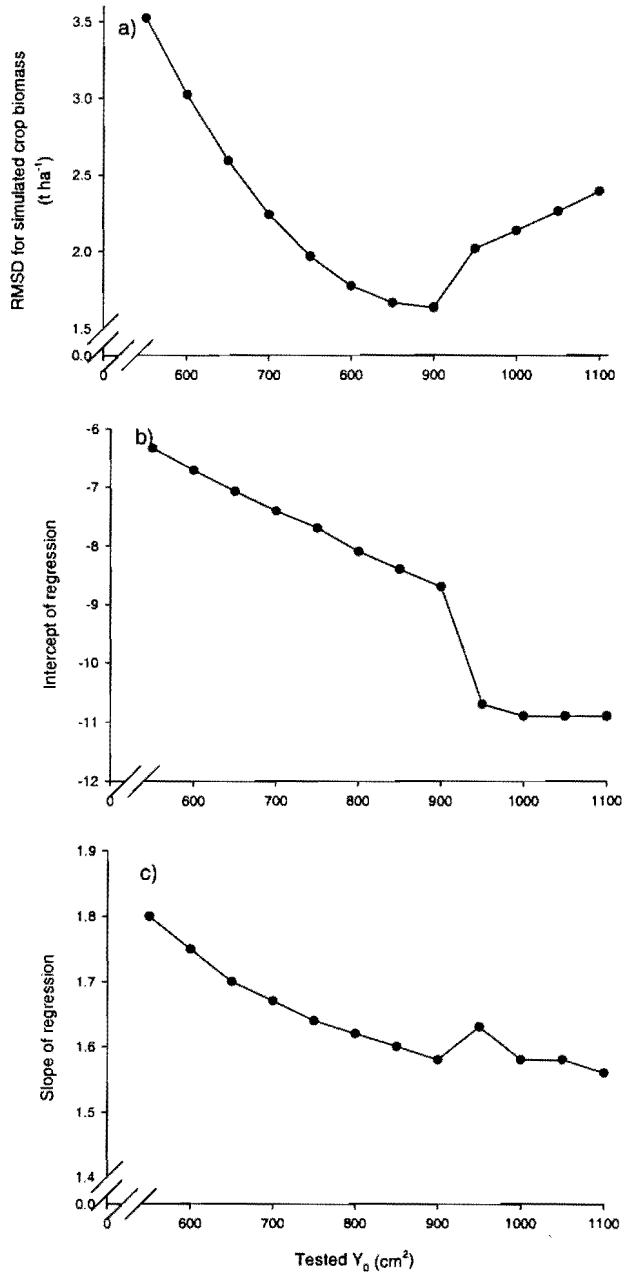

Figure 7.4 Sensitivity analysis of RMSD (a), intercept of regression (b) and slope of regression (c) for simulated crop biomass to values of Y_0 from 550-1100 cm^2 in 'Challenger' sweet corn grown in three experiments in New Zealand (Table 7.2).

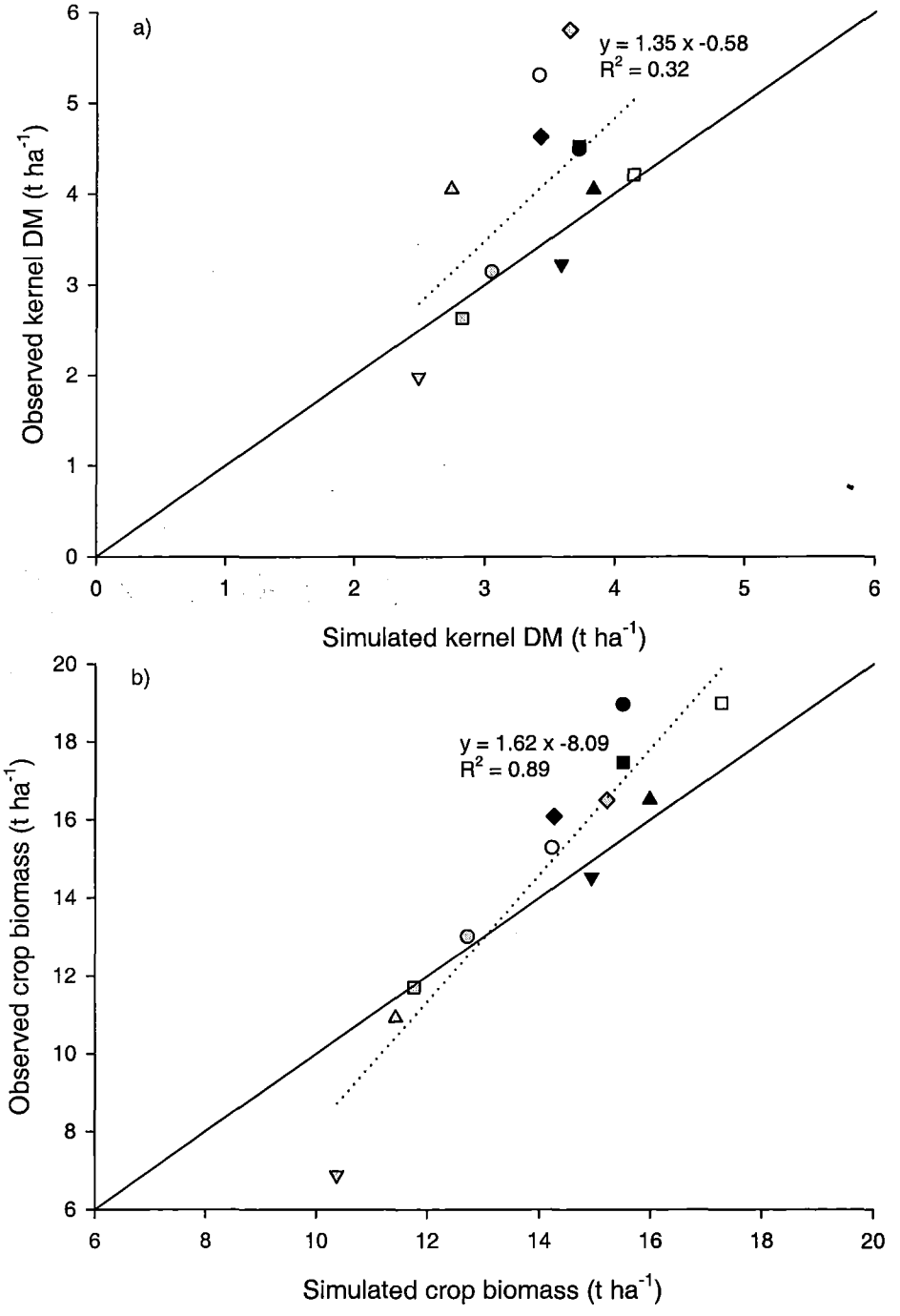

Figure 7.5 Comparison of simulated (assuming Y_0 = 800 cm^2) and observed values of kernel yield (t ha^{-1}) (a) and crop biomass (t ha^{-1}) (b), for 'Challenger' sweet corn grown in the experiments outlined in Table 7.2. The RMSD for (a) is 1.04 t ha^{-1} and for (b) 1.78 t ha^{-1}. (Symbols as in Figure 7.3).

7.3.2.2 Test 2

Using Olsen P as an input parameter there was close agreement between simulated and observed data for both kernel DM yield and days to canning maturity using the unmodified model (i.e. the asymptotic value of $Y_0 = 543$ cm^2) (Figure 7.6). This test was confounded because the model variables were developed from the same data with which it was then tested. Nevertheless, this test showed that the five empirical modifications to variation in P supply were sufficient to encapsulate the bulk of the variation in observed kernel yield (Figure 7.6a) and crop phenology (Figure 7.6b) in both Experiments 1 and 4. Simulated kernel DM yields had an RMSD of 0.45 t ha^{-1}, and days to maturity had an RMSD of 3.3 days. There was systematic variation in the latter i.e. in 2002/03 crop maturity was later than that predicted. This was most likely due to an uncoupling of the temperature data between Broadfields' and the experimental site in 2002/03 (Section 4.4.5.1).

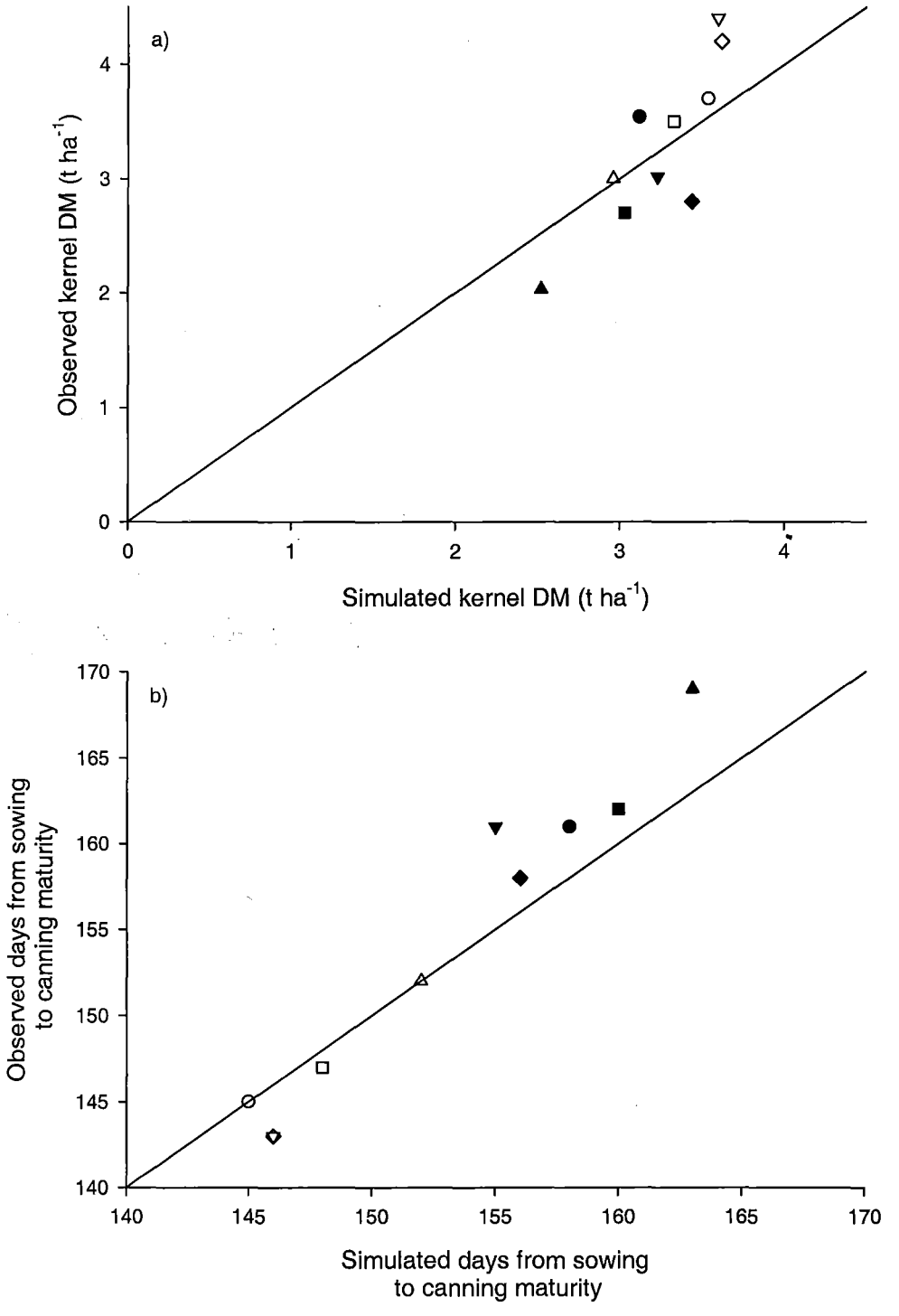

Figure 7.6 Comparison of simulated and observed values for kernel DM (t ha^{-1}) (a), and crop maturity (days after sowing) (b) for 'Challenger' sweet corn grown at Lincoln, Canterbury, New Zealand in 2001/02 and 2002/03 at five rates of fertiliser P. (Symbols in Table 4.1). The solid lines represent 1:1 relationships and are provided for comparison.

7.3.3 Long-term simulations

7.3.3.1 Yield simulations

The long term simulations gave a wide range of kernel yields depending on site, season, sowing date and P supply. As expected, crops with Olsen P = 6 μg ml^{-1} had lower simulated yields than crops that had a greater P supply. For example, at Lincoln from a 31 October sowing date mean simulated kernel DM yields were 3.2 t ha^{-1} with Olsen P = 6 μg ml^{-1}, 3.6 t ha^{-1} with Olsen P = 10 μg ml^{-1}, 4.1 t ha^{-1} with Olsen P = 20 μg ml^{-1}, and 4.2 t ha^{-1} with Olsen P = 30 μg ml^{-1} (Figure 7.7a).

Hastings crops had greater simulated kernel DM yields than Lincoln crops regardless of sowing date and P supply. For example a crop with Olsen P = 30 μg ml^{-1} sown on 31 October gave a mean simulated kernel DM yield of 4.2 t ha^{-1} at Lincoln (Figure 7.7a) and 4.4 t ha^{-1} at Hastings (Figure 7.7b).

The delay in sowing from 31 October to 30 November decreased simulated kernel DM yields for both sites and across P supplies. However, the reduction was greater at Lincoln than at Hastings. When Olsen P = 30 μg ml^{-1} the mean simulated kernel DM yield at Lincoln decreased from 4.2 t ha^{-1} from 31 October sowing (Figure 7.7a) to 3.5 t ha^{-1} from 30 November sowing (Figure 7.7c), a 17% decrease. Hastings simulated kernel DM yields decreased from 4.4 t ha^{-1} (Figure 7.7b) to 4.0 t ha^{-1} (Figure 7.7d) for these same sowing dates (a 10% decrease).

Variation in season caused greater variation in simulated yields than did variation in P supply. This can be observed from the spread of each of the probability of exceedance distributions. For example, simulated crops sown on 31 October at Hastings, with Olsen P = 30 μg ml^{-1} had

a mean simulated kernel DM yield of 4.4 t ha^{-1}, with simulated yields ranging from 2.9 t ha^{-1} to 5.2 t ha^{-1} (Figure 7.7b).

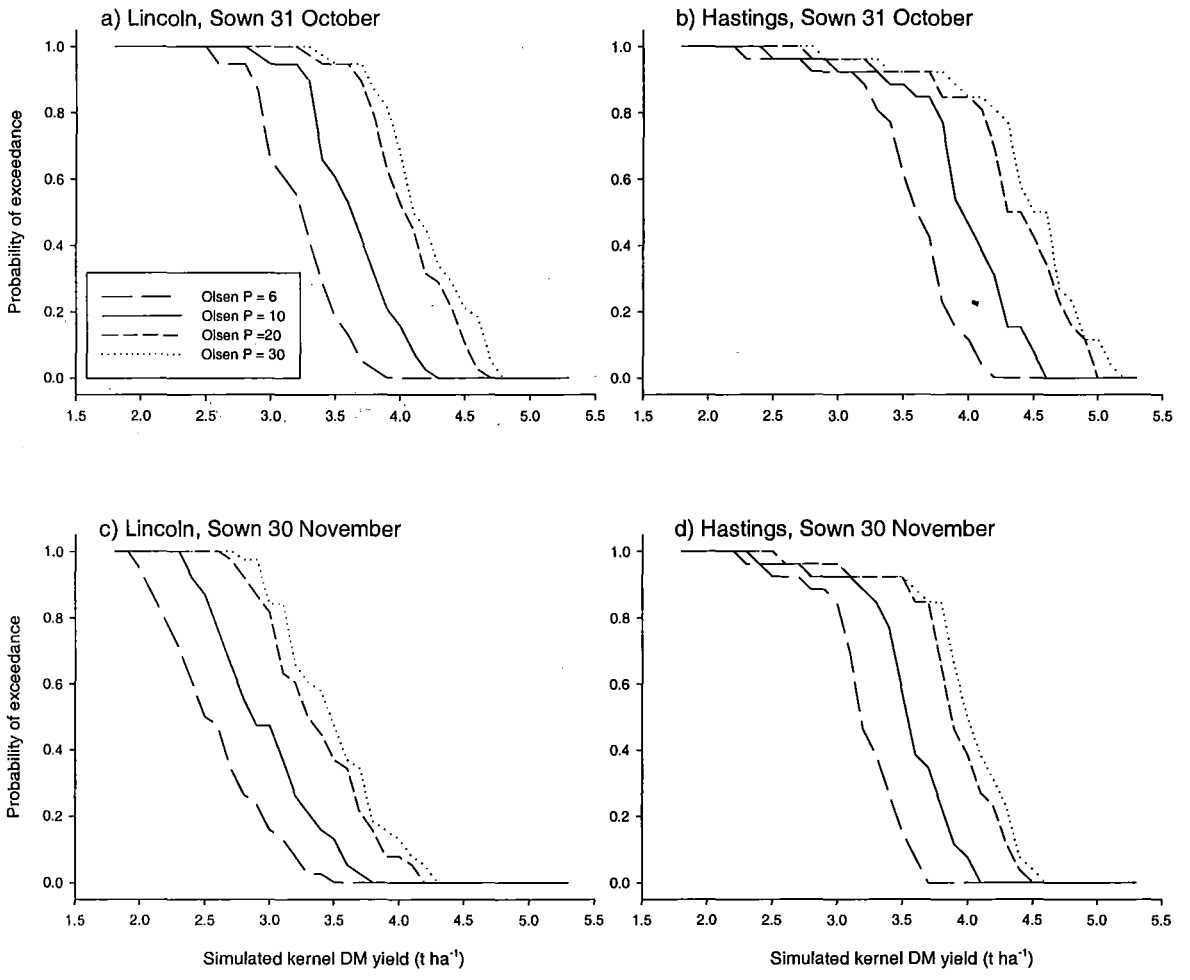

Figure 7.7 Simulated (assuming asymptotic value of Y_0 = 800 cm^2) long term probability of exceedance distributions for kernel DM yield (t ha^{-1}) of 'Challenger' sweet corn sown on 31 October at Lincoln (1960-2002) (a), and Hastings (1976-2001) (b); and sown on 30 November at Lincoln (c), and Hastings (d) with four levels of available soil P (Olsen P = 6, 10, 20, and 30 µg ml^{-1}; line styles outlined in the legend of (a)).

7.3.3.2 Maturity simulations

At Lincoln the simulated probability of 'Challenger' crops failing to reach canning maturity before the first autumn frost increased markedly with each delay in sowing (Figure 7.8a). Crops where P supply was limited (6 μg ml^{-1}) had a consistently greater (by ~0.1) probability of failure compared with the 30 μg P ml^{-1} crops. With Olsen P = 6 μg ml^{-1} there was a risk of failure of 0.13 from a 15 October sowing date and for Olsen P= 30 μg ml^{-1} there was a risk of 0.05 for the same sowing date. For every 10 day delay in sowing there was approximately a 0.11 increase in risk for both crops, and all crops reached a risk of 1 (i.e. all simulated crops failed) from a 3 January sowing date (Figure 7.8a).

In contrast there was a comparatively minor risk of crop failure at Hastings. Risk was negligible (<0.1) for all crops sown before 10 December. Risk then increased to ~0.4 and was comparatively greater in the 6 μg P ml^{-1} crops compared with the 30 μg P ml^{-1} crops (Figure 7.8b).

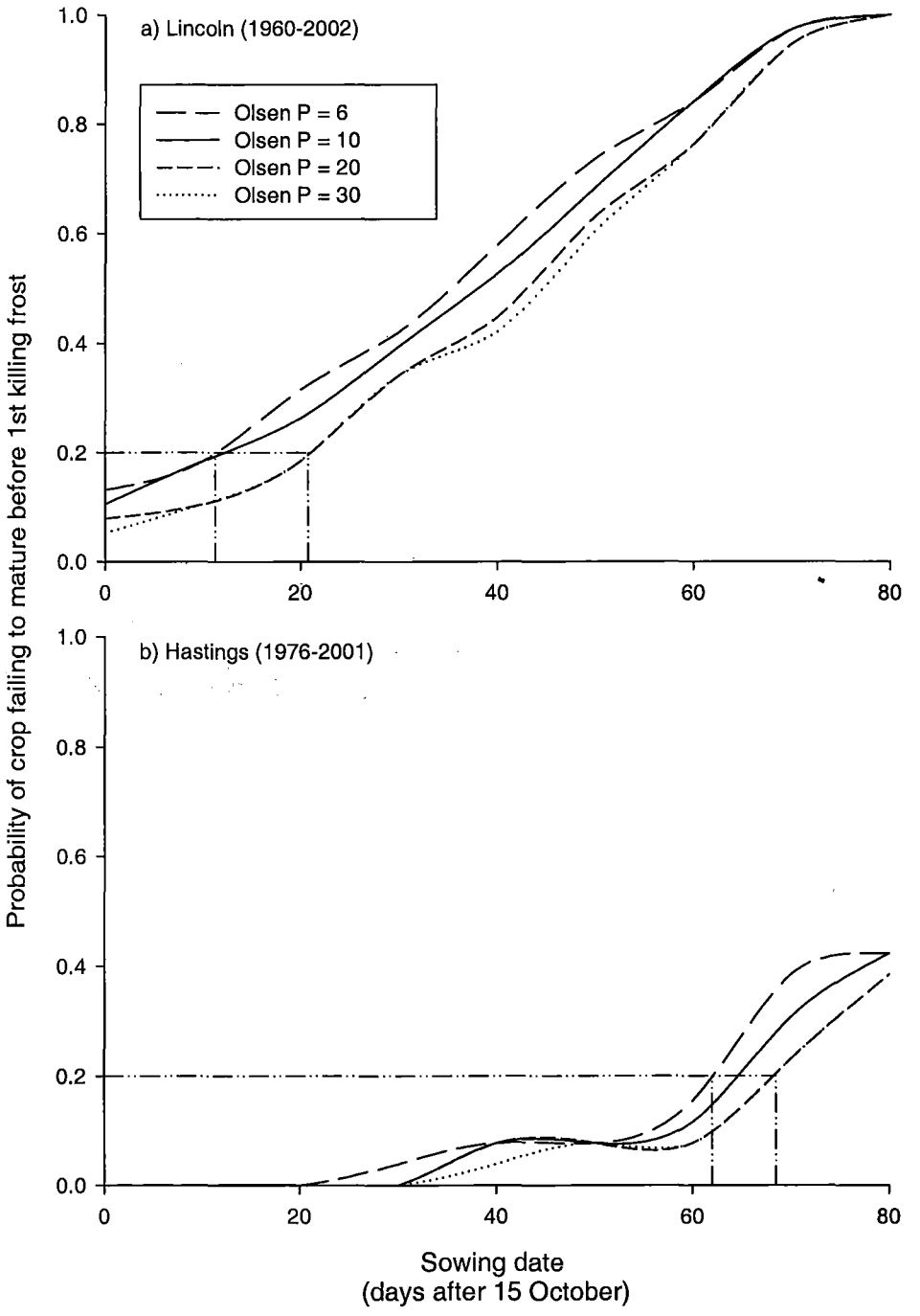

Figure 7.8 Simulated long term probabilities for failure of 'Challenger' sweet corn to reach canning maturity (72% kernel moisture) before the first autumn frost at Lincoln (1960-2002) (a) and Hastings (1976-2001) (b), at four levels of P supply (Olsen P = 6, 10, 20, and 30 μg ml^{-1}). Treatments are shown in the legend. The drop lines indicate where risk of crop failure is 0.2 and are described in the discussion.

7.4 Discussion

7.4.1 Model development and testing

The testing of this model in response to P supply (Figure 7.6) indicated that most of the variation in kernel yield and crop development in the current data set (Experiments 1 and 4) could be described by altering five coefficients of the crop model in response to P supply (Figure 7.1 and Figure 7.2). However, the results were confounded because the test was performed with the same crop with which the model was developed. A more rigorous test based on independent data, preferably from another region, is required.

An independent test of the model was only possible for potential yields, when P supply was non-limiting, based on the data sets from Hastings and Lincoln (Table 7.2). These showed that the framework was sufficiently robust to encapsulate the yield trends across three seasons at two locations and a variety of sowing dates (Figure 7.3). The model consistently under predicted kernel yields, probably due to the area of the individual leaves being too low. This then had a profound effect on GLAI and hence simulated crop and kernel biomass. Indeed the optimised model based on Y_0= 800 cm^2 showed a marked improvement in predicted crop DM (RMSD = 1.78 t ha^{-1}) in simulated kernel yield (Figure 7.5b). The implication was that there was some other environmental factor limiting leaf area e.g temperature, light or plant population (Bos *et al.*, 2000a; Bos *et al.*, 2000b). Alternatively, incorrect RUE may also have caused the under prediction of crop biomass (Figure 7.3). However, given that RUE is relatively stable for a crop in unstressed environments (Sinclair and Muchow, 1999) it is unlikely that this was the case. It may have been that the RUE response to temperature (Equation 7.2) was too severe. However, previous research has shown that this function was appropriate (Wilson *et al.*, 1995). Furthermore, other research has demonstrated a similar sensitivity of RUE to temperature in maize (Andrade *et al.*, 1993; Andrade *et al.*, 1992).

Therefore, an incorrect assumption about individual leaf area was the most likely cause of the under prediction of crop biomass (Figure 7.3).

A simulation model based on the uptake and distribution of P within individual plants would be a more mechanistic approach to simulating yields in response to P supply. A similar approach to that used by Sinclair and Muchow (1995) with N supply in maize would seem appropriate. In this approach a minimum SLP (0.1 g P m^{-2}) (Figure 6.4) would be set and used to modify GLAI. RUE was not affected by P supply and hence would not need to be altered provided that SLP was above 0.1 g P m^{-2}. This approach would be desirable because it could potentially account for interactions between N and P supply when used in conjunction with the N supply model of Sinclair and Muchow (1995). The consistent relationship between SLP and SLN demonstrated in Figure 6.2 indicates that a simple 'law of the minimum' approach would be sufficient to simulate *Zea mays* crops where both or either N and P supply are limited.

Harvest index varied from 0.21 to 0.37 in the experimental data sets tested here. However, the model used a single HI of 0.24 and consequently gave poor estimates of kernel yield (Figure 7.5a). These changes in HI may have been associated with differences in harvest time of individual experiments and consequently an increase in HI with time would have been more appropriate than a single value of HI. Therefore a more comprehensive model would include a function for a linear rate of increase of harvest index with either days (Muchow *et al.*, 1990) or thermal time (Stone *et al.*, Unpublished; Wilson *et al.*, 1995).

Such a model would require a detailed P uptake module. However, the uptake of P from the soil is a complex process depending on root densities, pH, P retention characteristics of the

soil, soil temperature, soil water, P fertiliser forms, and mychorrhizal associations. Furthermore soil P occurs in various pools, such as soil-solution P, labile P, non-labile P, and organic P. The sizes of these pools vary with soil type. For example the plant unavailable fraction may be between 20 and 80% of the total P (Schachtman *et al.*, 1998). Consequently simulating P uptake from a field requires detailed soil data that were not collected and are beyond the scope of this study. Linking the data from the current experiments with a detailed analysis of sweet corn P uptake would be the next step in investigating yield responses to P supply. For example a soil P module similar to that used in APSIM (McCown *et al.*, 1996) may be applicable.

7.4.2 Long term simulations

7.4.2.1 Yield simulations

Simulated yield distributions in Figure 7.7 show that a single asymptotic response curve (e.g. Figure 4.1) was insufficient to adequately describe kernel yield responses to P fertiliser supply. Simulated kernel yields varied depending on site, sowing date and P supply (based on Olsen P). However, the greatest source of variation in kernel yield was between seasons, which were associated with air temperature and solar radiation fluctuations.

For example in Figure 7.7b the long term mean kernel DM yield at Hastings from 31 October sowing was 4.4 t ha^{-1} with Olsen P = 30 μg ml^{-1} with seasonal yields ranging from 2.9 to 5.2 t ha^{-1}. If the yield at 90% and 10% probability of exceedance was taken then it can be predicted with 80% certainty that kernel yields would be between 3.9 and 5 t ha^{-1}. However, if Olsen P = 6 μg ml^{-1} the 80% distribution was between 3.2 and 4 t ha^{-1}. This analysis shows the advantage of using a long-term simulation approach to describe yield. It allows a sweet corn producer to make informed decisions and plan based on probable yields. In contrast, a single asymptotic response curve only enables decisions to be based on a single result set, which is

not necessarily relevant to the season in question. A modelling approach therefore represents a more rigorous description of yield response to P.

In reality the nature of these simulated results is more theoretical than practical. This is because low soil P status is generally rare on intensively cropped land in New Zealand. This is highlighted in a recent survey of 51 sweet corn crops in Gisborne, Hawkes Bay and Hamilton in New Zealand where more than 70% of crops had a soil Olsen P of greater than 15 $\mu g\ ml^{-1}$ (P. Stone *Pers. comm.*). Soil P levels are generally adequate due to the widespread historical use of phosphate based fertilisers. Additionally when cropping farmers become aware of a P limitation they generally correct them immediately using fertilisers.

The long term simulations (Figure 7.7) showed some interesting trends. Firstly yields would be consistently greater with higher levels of available P. This is not surprising given the model structure. Secondly simulated yields were consistently greater at Hastings compared with Lincoln. This was due to the ~ 2.0°C warmer mean daily air temperatures at Hastings (Table 7.3). Increased temperatures had two effects, leaves appeared at a faster rate and hence GLAI establishment was more rapid, resulting in an increase in RI_{cum}. The greater temperatures also meant that RUE was increased (Wilson *et al.*, 1995).

A third trend was that delayed sowings decreased yields at both Lincoln and Hastings. This has been demonstrated experimentally at Hastings (Rogers *et al.*, 2000). In both climates peak GLAI is always after the maximum incoming solar radiation and hence delayed sowings mean the asynchrony between GLAI and incoming solar radiation curves is increased and yields are reduced (Rogers *et al.*, 2000; Stone *et al.*, 1998b). This simulation analysis demonstrates that the results of Rogers *et al.* (2000) are valid at both Hastings and Lincoln and also over many

seasons. To examine this trend, long term kernel yields were simulated at Hastings from sowing dates of 31 Oct to 20 Dec at 10 day intervals for both a 30 and 6 μg P ml^{-1} 'Challenger' crop with a plant population of 60000 ha^{-1}. For every 10 day delay in sowing there was a decrease in predicted kernel DM yield of 0.15 t ha^{-1} for both P supplies (Figure 7.9).

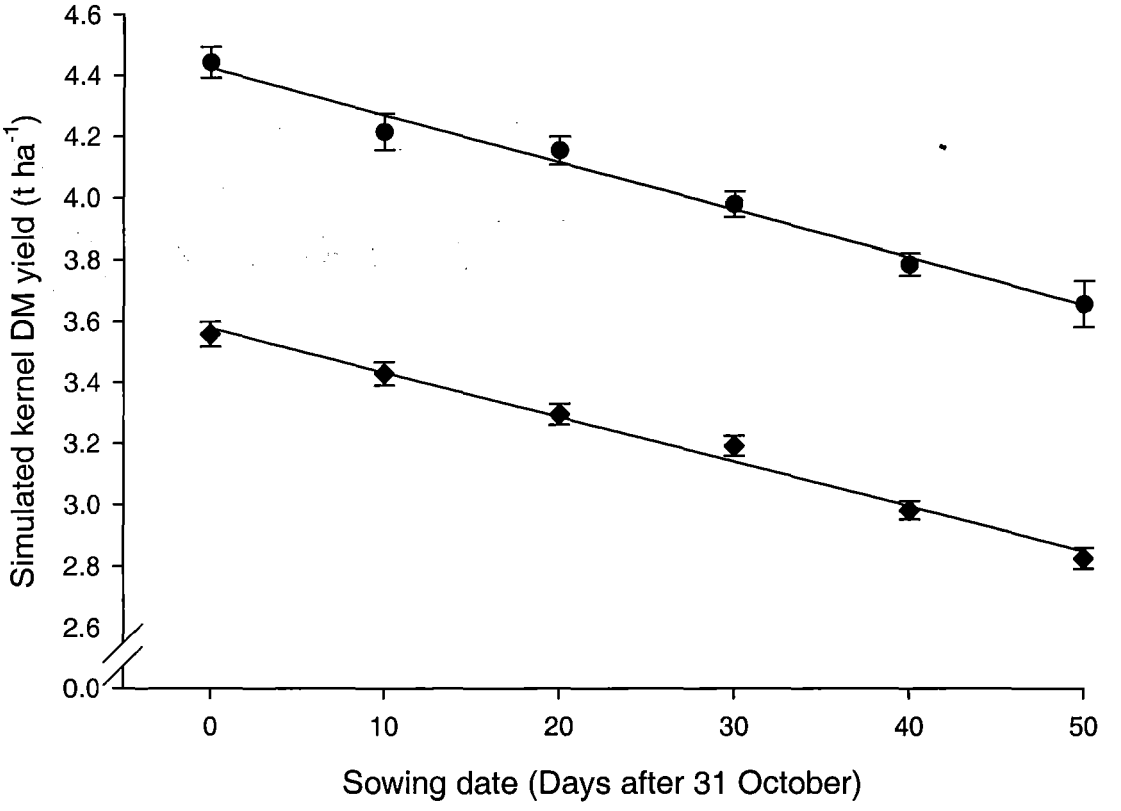

Figure 7.9 Long term (1976-2002) simulated kernel DM yield (t ha^{-1}) of 'Challenger' sweet corn grown at Hastings from sowing dates of 31 October, 10, 20, 30 November, 10 and 20 December. There were two crops with an Olsen P of either 30 μg ml^{-1} (•) or 6 μg ml^{-1} (♦) with a plant population of 60 000 ha^{-1}. The error bars represent the standard error of the means. The regression equations are: for Olsen P = 30, $y = 4.42 - 0.015x$; $R^2 = 0.98$ and for Olsen P = 6, $y = 3.58 - 0.015x$; $R^2 = 0.99$.

This simulation approach to describing phosphorus kernel yield responses can also answer pertinent crop management questions. The yield response to P fertiliser was due to an increase in RI_{cum} with conservative RUE (Section 6.4.1). Therefore, some of the lost productivity could potentially be compensated for by some other management factor increasing GLAI in these low P crops. One option is to increase plant population. Using a 30 November sowing date and a plant population of 60 000 plants ha^{-1} at Lincoln the mean kernel DM yield with Olsen P = 30 μg ml^{-1} would be 3.5 t ha^{-1}. If Olsen P = 6 μg ml^{-1} this yield would be 2.6 t ha^{-1} (Figure 7.7c). To offset this loss with Olsen P = 6 μg ml^{-1} the population would need to be doubled to ~120 000 plants ha^{-1} (Figure 7.10). Experimental validation of these results is necessary as extremely high plant populations may alter some of the coefficients relating to leaf expansion and leaf appearance (Bos *et al.*, 2000a). Furthermore, increasing plant populations may adversely affect sweet corn ear and kernel quality (Stone *et al.*, 1998a). Nevertheless at least some of the lost yield with nutrient deficiencies could be offset by increasing plant populations.

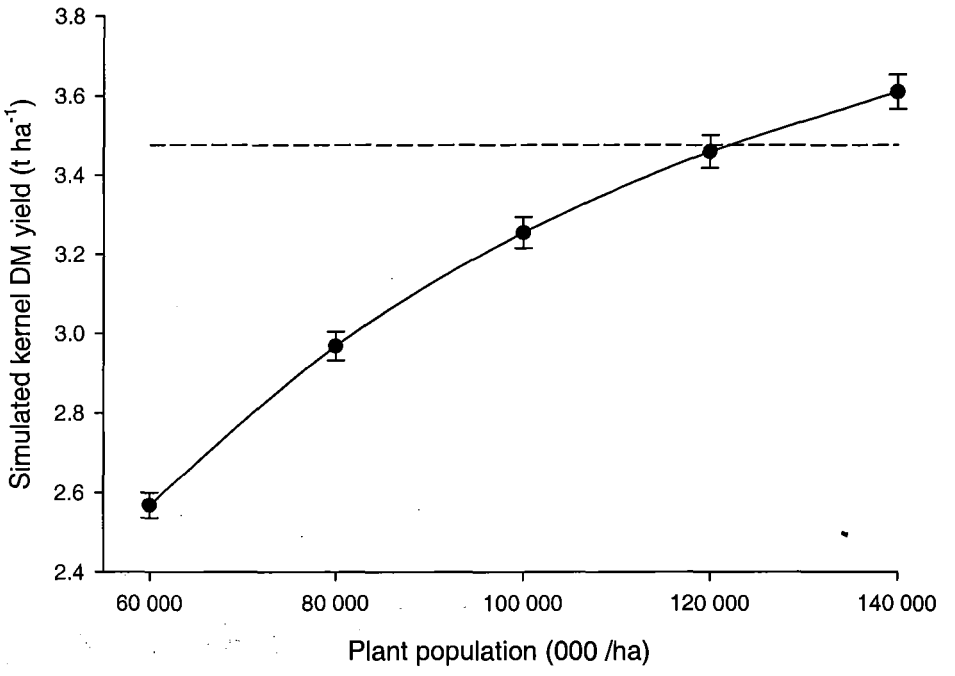

Figure 7.10 Long term (1960-2002) mean simulated kernel DM yield (t ha-1) of 'Challenger' sweet corn grown at Lincoln from a 30 November sowing date, with Olsen P = 6 μg ml^{-1}, at five plant populations (60 000, 80 000, 100 000, 120 000, and 140 000 plants ha^{-1}). The error bars represent the standard errors of the means. The dotted line is mean (1960-2002) simulated kernel yield with Olsen P = 30 μg ml^{-1} at 60 000 plants ha^{-1} at Lincoln from 30 November sowing date.

7.4.2.2 Maturity simulations

This long-term yield analysis assumed that crops were not killed by frosts occurring before maturity. However, the development study showed that the risks to crop production with limited P supply were also associated with an increased risk of crops failing to mature before the first killing frost (Figure 7.8). This was more important at Lincoln (Figure 7.8a) than at Hastings (Figure 7.8b), due to lower temperatures (less Tt accumulation) and earlier frosts. Subsequent discussions concentrate on the Lincoln results.

From a 15 October sowing there was a minor risk (0.05-0.15) of crop failure associated with rare events of mid to late March frosts for all P levels at Lincoln. As expected, delaying sowing past 15 October increased risk at Lincoln (Wilson and Salinger, 1994) due to a delayed crop maturity. The later maturity for the P = 6 μg ml^{-1} crops meant that the risk was consistently greater than the P = 30 μg ml^{-1} crops. A crop sown on 24 November at Lincoln with P = 6 μg ml^{-1} crop would have a risk of 0.58 and for P = 30 μg ml^{-1} crop this would be 0.42 (Figure 7.8a).

Again this simulation approach allows growers to make informed decisions based on long-term probabilities. For example, if a sweet corn grower near Lincoln decided that a 0.2 risk of crop failure was the limit of acceptable risk, then a P = 30 μg ml^{-1} crop should be sown before 5 November and a P = 6 μg ml^{-1} crop before 26 October to maintain this probability (Figure 7.8a). A Hastings grower should sow a 30 μg P ml^{-1} crop before 22 December and a 6 μg P ml^{-1} crop before 16 December (Figure 7.8b) to preserve this probability.

The principles in this maturity risk analysis are not specific to sweet corn grown in Canterbury. Any crop species grown where the season length is limited (by either temperature or water supply), is at risk of not maturing during the favourable growing season. Delayed sowings or a nutrient deficiency that delays crop maturity will increase this risk.

7.5 Conclusions

- The simple framework used to simulate 'Challenger' sweet corn growth and development predicted the responses to P supply well. However, there was some discrepancy with the equations used to describe individual leaf area. For example, Y_0 needed to be increased to 800 cm^2 from 550 cm^2 to accurately simulate crop DM. This is an aspect of crop growth that requires further investigation and the current value of Y_0 represents the best answer based on the sensitivity analysis carried out here.
- These tests confirmed that the bulk of the variation in kernel yield in Experiments 1 and 4 was associated with the effects of P nutrition on leaf appearance and individual leaf area.
- The long-term yield simulations confirmed that a single asymptotic response curve was inadequate for describing the response of 'Challenger' sweet corn yield to P supply. There were large variations in simulated yields between sites and sowing dates. The greatest variation in simulated yields was between seasons.
- The analysis of the risk of 'Challenger' crops failing to mature before the first killing autumn frost showed that the risk was greatest at Lincoln. This risk was increased by delayed sowings and by lack of sufficient P supply. The difference in risk meant that to obtain an equal long term risk of crop failure a 6 μg P ml^{-1} crop would need to be sown 10 days before a 30 μg P ml^{-1} crop.

Chapter 8. General discussion and conclusions

The aim of this thesis was to examine HI, RI_{cum} and RUE from Equation 1.1 for 'Challenger' sweet corn and determine those that responded to a limited N and P supply. There was only a minor response to N supply as described in Chapter 4 and therefore this was not examined further. Effectively the N responses were analogous to the response of the 200 kg P ha^{-1} crops in Experiment 1. In contrast, there was a strong response of both crop DM and kernel yield to variable P supply. The analyses in Chapters 4-7 showed that these changes in kernel yield and crop DM were predominantly due to a reduced RI_{cum}, with RUE and DM partitioning largely unchanged. These results are consistent with previous results for maize (Plenet *et al.*, 2000a; Plenet *et al.*, 2000b).

8.1 Agronomic implications

In Chapter 4 the N and P treatments produced a range in total crop DM from 9.7 to 17.5 t ha^{-1} (Figure 4.1). This was partitioned conservatively, as ~24% kernels, 44% leaves and stems, and 32% ears regardless of N or P rate (Figure 4.2). There was also a consistent relationship between the harvestable ears m^{-2} and total crop DM (Figure 4.3 a).

The yield response to P fertiliser is consistent with the Olsen P of 6 μg ml^{-1} and the recommended value of >35 μg ml^{-1} for sweet corn (Clarke *et al.*, 1986). Commercial crops are unlikely to be grown at the fertility levels used in this research. However, these were required to examine, in subsequent chapters, the mechanisms responsible for the kernel yield responses to P. Such responses are also relevant to moderate P limitations. Due to conservative partitioning the kernel yield mirrored the response of total crop DM to P.

Ear quality was altered by P supply. The key measures of ear quality were unfilled tip length, ear diameter, and individual kernel DM. These were all closely related to the kernel yield per ear (Figure 4.4, Figure 4.5). This was consistent with previous experiments with P stress (Section 2.4), N stress (Stone *et al.*, 1998a), water deficits (Stone *et al.*, 2001a) and sowing dates (Rogers *et al.*, 2000), in which reductions in some or all of these traits were associated with reduced kernel yields.

The general agronomic implication of these results is that to maximise crop value, through improvements to kernel yield and ear quality, growers should manage P fertiliser to achieve maximum total crop DM. The economically optimum P fertiliser rate will dépend on the cost of fertiliser, the expected kernel DM response, the price of sweet corn, and the premium for high quality ears.

8.2 The role of P in determining sweet corn yield

The focus of this thesis then moved to examining the mechanisms by which P deficiency had decreased total crop DM of 'Challenger' sweet corn. The first step was a detailed analysis of RI_{cum}. In Chapter 5 it was calculated that RI_{cum} was ~25% less in the 0 kg P ha^{-1} crops than in those receiving non-limiting P fertiliser rates (Figure 5.13 and Table 5.4). This was caused by reductions in both leaf appearance rate (Figure 5.2 and Figure 5.5) and individual leaf area (Figure 5.7 and Table 5.2), which is in accordance with previous literature (Colomb *et al.*, 2000; Plenet *et al.*, 2000a; Plenet *et al.*, 2000b). The sensitivity analysis (Table 5.5) confirmed that both of these processes were responsible for the reduction in RI_{cum}. Therefore, attempts to model crop responses to P should focus on the development of GLAI (Pellerin and Mollier, 2001) and both individual leaf areas and leaf appearance rates will be central to this process (Rodriguez *et al.*, 1998a).

Crop RUE was analysed in Chapter 6 and found to be conservative across P treatments and modified in accordance with the temperature function proposed by Wilson *et al.* (1995). However, during establishment (<10 fully expanded leaves) RUE was approximately half that found during the main growth period for all crops examined. The physiological mechanisms of this result were unclear and warrant further examination. It seems likely that an increased partitioning of crop DM to roots during early crop stages (Tollenaar, 1989b) is at least partially responsible for this observation. A lower photosynthetic capacity of the initial leaves (Thiagarajah *et al.*, 1981) may also be implicated.

8.3 Long term simulations of yield and development

In Chapter 7 the responses from Chapters 5 and 6 were used to compile long term yield probabilities for 'Challenger' sweet corn crops when grown at Lincoln or Hawkes Bay with varying soil P. The maize simulation framework described by Muchow *et al.* (1990) was modified to respond to P. This analysis confirmed that a single response curve was inappropriate for multiple sites and seasons (Figure 7.7). The environment was important in controlling responses to P. Growers could use these long-term simulated probabilities to make informed P fertiliser decisions.

Chapter 7 also examined the implications of a delay in crop maturity when P was limited (Table 4.2). This increased the risk of a crop failing to mature before the first killing frost by ~10% over a fully fertilised crop in Canterbury. Growers should consider soil fertility when choosing appropriate sowing dates particularly in Canterbury, but in Hawkes Bay this effect was minimal and predicted to be of minor practical importance.

The model in Chapter 7 is only a preliminary step towards a model of sweet corn response to P and is intended only to demonstrate the variation in expected yields. Further development

and testing is required, especially a re-examination of the individual leaf areas, given the difficulties in accurately measuring them in this study (Appendix 10).

8.4 Physiological effects of P on plant and crop growth

The results of the current study are in general agreement with the conclusion of Pellerin and Mollier (2001) that P affects maize growth through a direct role in leaf area expansion and other processes are source limited due to this effect (Figure 8.1). This contrasts with the modelling approach used in APSIM (McCown *et al.*, 1996) where the dominant effect of P was on photosynthesis (Probert, 2004). These APSIM modules simulated maize responses to P well (RMSD = 1.58 t ha^{-1}) (Kinyangi *et al.*, 2004). GLAI or RI data were not reported, and it is possible that the correct yields were simulated using an incorrect mechanism.

This thesis mostly agrees with Pellerin and Mollier (2001), but in the first leaves the photosynthetic rate was reduced (Figure 6.5). This was probably a factor of the small root system early in the crop limiting P uptake and resulting in acute P stress. The consistency of the bell shaped curves (Figure 5.7 and Table 5.2) suggests that the individual area of upper leaves was limited by the area of the leaves lower in the canopy and not directly limited by current P status. This is consistent with previous maize research where Y_0 responded to different soils and seasons (550 – 770 cm^2) (Dwyer and Stewart, 1986a); water deficits (540-750 cm^2) (Stone *et al.*, 2001b); or liming treatments (~400-700 cm^2) (Sierra *et al.*, 2003) but the position (X_0) and shape (b and c) of these curves were unaffected. The area of an individual leaf depended on the area of the leaves immediately below it (Dwyer and Stewart, 1986a). The total leaf area below a given leaf determines RI_{cum}, and hence plant growth rate, during the expansion of that given leaf. Thus, the first leaf on a maize plant is the smallest as its expansion depends on seed reserves. The second leaf is slightly larger as the RI_{cum} by the

first leaf determines its expansion. The third leaf is larger still, and the individual leaf area continues to increase in an approximately exponential relationship with leaf position until the largest leaf expands (X_0). After this more of the assimilate produced is used to produce reproductive structures (ears, tassels etc) and individual leaf areas begin to decrease.

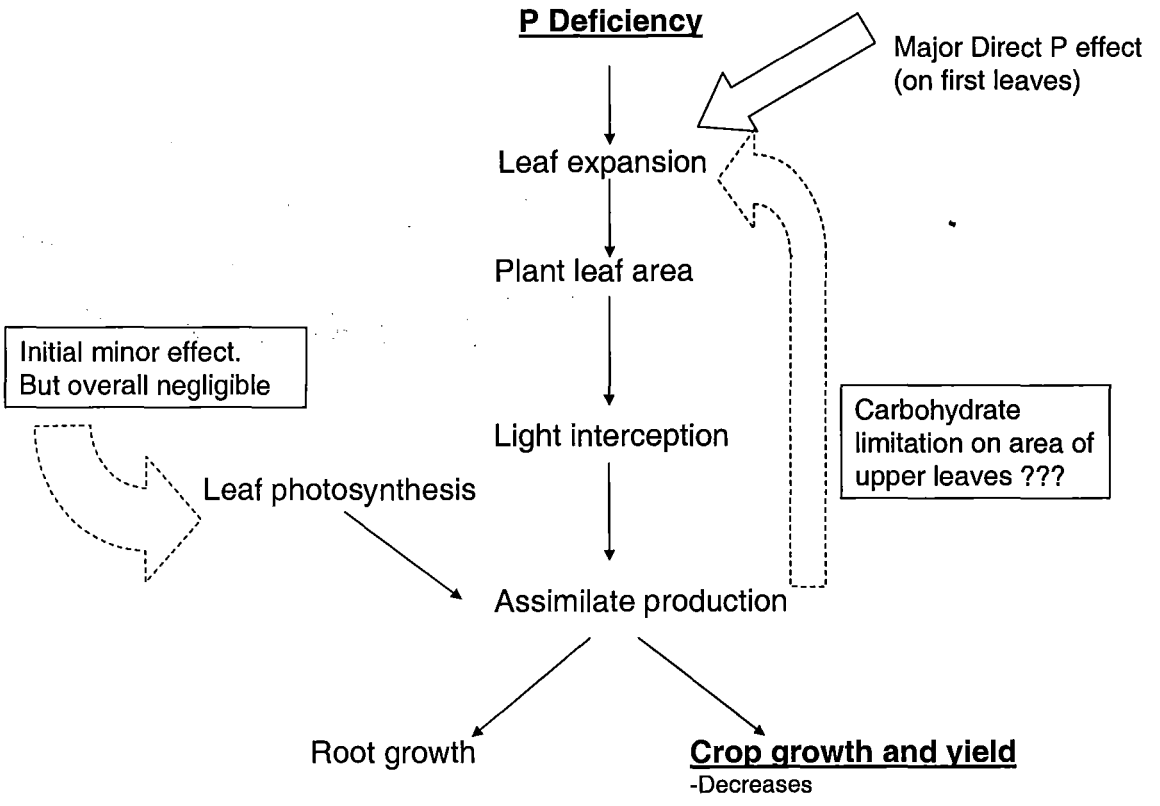

Figure 8.1 Summary of the interpretation of the role of P deficiency in reducing the overall growth of 'Challenger' sweet corn (After Mollier and Pellerin, 1999; Pellerin and Mollier, 2001). The key processes that differ from Pellerin and Mollier (2001) are indicated by the dotted arrows and the text boxes, other interpretations are in common with Pellerin and Mollier (2001).

The wide range of SLP from 0.1-0.3 g P m^{-2} over which P_{2000} did not change suggests that further increases in SLP above 0.1 g P m^{-2} did not enhance photosynthesis. However, the low

R^2 in Figure 6.4 suggests that further detailed research is needed to confirm this response. This is consistent with a non-metabolic pool of P stored in the vacuoles, acting as a buffer against subsequent P limitations (Grant *et al.*, 2001). The maximum SLP found in the 0 kg P ha^{-1} crops was 0.19 g P m^{-2} for leaf 15, which had an area of ~170 cm^2 compared with 280 cm^2 for a 200 kg P ha^{-1} leaf at the same position (Figure 5.7). The 0 kg P ha^{-1} leaf could have obtained an area of 280 cm^2 while still maintaining an SLP of 0.12 g P m^{-2}, which is above the proposed critical level of 0.1 g P m^{-2} for photosynthesis. This further suggests that the expansion of this leaf was not responding to the current P status but was reduced by some other factor probably operating during leaf initiation or during early expansion.

The simplest explanation of this would be a carbohydrate limitation. Decreased light intensity, temperature, increased plant density (Bos *et al.*, 2000a; Bos *et al.*, 2000b) and defoliation (Johnson, 1978) have all been shown to limit the area of individual maize leaves. However, Rodriguez *et al.* (2000) showed that water soluble carbohydrates accumulated in P deficient wheat leaves, indicating that carbohydrate was not limiting. A simulation analysis demonstrated that a carbohydrate limitation was unlikely to cause the reduced leaf area in P deficient wheat (Rodriguez *et al.*, 1998b).

In the current study, it is likely that the area of individual leaves was limited by the reduced carbohydrate supply during the period of rapid cell division of each leaf and not the carbohydrate during the full period of leaf expansion. This is when the leaf is heterotrophic. Thus, the area of the upper leaves probably depended on the area of the leaves below them. For example, the total PPFD absorbed by sunflower plants during the period of rapid cell division of leaf 8 limited the expansion of leaf 8 (Granier and Tardieu, 1999). This initial phase of cell division occurs when the leaf is heterotrophic. Following this the leaf is

autotrophic (Tardieu *et al.*, 1999). Muller *et al.* (2001) showed that a 4 day shading treatment decreased the relative expansion rate of maize leaves. However, because the shading period was short and discrete the effect on final leaf length was minor. Continuous shading may have severely reduced leaf length even though the relative expansion rate may have recovered once the leaf became autotrophic. The absolute expansion rate would then be decreased due to the initial decrease in relative expansion.

This hypothesis, of the area of the upper leaves being limited by the plant growth rate during the period of rapid division of each leaf, is consistent with the mechanism of response for P deficient maize demonstrated by Assuero *et al.* (2004). In this experiment the size of the cell division zone, and hence the number of cells per leaf, was reduced when P supply was limited. In the current study the reduced radiation absorption per plant for this period of exponential cell division was caused by the smaller area of the leaves immediately below the expanding leaf. This also explains the slower leaf appearance rate in the 0 kg P ha^{-1} crops (Figure 5.2). Rapid cell division occurs before the appearance of each leaf tip. Therefore, the rate at which primordia extended to become visible leaf tips probably decreased when P was deficient.

This mechanism would explain why early P nutrition is important in maximising crop yield (Grant *et al.*, 2001). Specifically, insufficient P during early crop growth results in a reduced area of the first leaves, giving a subsequent reduction in leaf area development, which means that crops do not recover from this initial P deficiency. The overall effect is that RI_{cum} is reduced in P deficient crops and hence overall yield is reduced. A practical interpretation of this phenomena is that an adequate P supply to maize before the six leaf stage is critical to

obtaining maximum yields (Barry and Miller, 1989) and yield responses are closely associated with the shoot P concentration at the 4-5 leaf stage (Lauznon and Miller, 1997).

The importance of early season P can be explained by its uptake mechanism, which is primarily diffusion (Barber *et al.*, 1963). A difficulty for uptake is that diffusion of P occurs over small distances of ~0.5 mm (Barber, 1977). Consequently, only P that is ≤0.5 mm from a root is absorbed. As crop development advances the soil volume explored by roots increases and hence increased amounts of P are positioned within 0.5 mm of a root even for crops grown on low P fertility soils.

8.5 Mechanistic modelling of P responses and their potential use

The model in Chapter 7 was based upon empirical relationships between individual crop processes (individual leaf areas and leaf appearance rates) and soil P tests. The intention was to demonstrate that yield responses to P fertiliser were site and season specific. This demonstrated a requirement to create a mechanistic model of P uptake, distribution within the plant, and its effect on growth. Such a model would be more globally applicable and consistent, and could predict growth and yield responses to P in a wider range of situations.

The responses to P supply in this thesis have provided results that could form the basis of future mechanistic models. Recently, two models have been described that include the capability to simulate crop responses to P (Daroub *et al.*, 2003; Probert, 2004). Their emphasis has been on simulating the process of P uptake, whilst simultaneously simulating the processes by which P stress affects crop growth using empirical 0 to 1 stress factors to modify growth. This approach simulates yields well (Daroub *et al.*, 2003; Kinyangi *et al.*, 2004), so these models may be appropriate for decision support systems. However, simulation models can also be used to summarise and test hypotheses about how crops grow (Section

1.2). To do this models should be physiologically based (Section 1.2) rather than use empirical 0-1 scaled stress factors.

The process of summarising and testing hypotheses using crop models is demonstrated by the investigation of RUE in maize. The hypothesis of potentially low RUE during establishment (Figure 6.7) was developed using crop models. Muchow *et al.* (1990) demonstrated that sub-tropical maize yields could be simulated using RUE = 1.6 g DM MJ^{-1} and concluded that the greatest yields would occur in cool climates with high incident solar radiation. Wilson *et al.* (1995) tested this hypothesis in a cool temperate climate and showed that the assumption of constant RUE was incorrect. They then proposed a modification of RUE for mean daily temperatures < 16 °C. In this thesis, the basic simulation of crop yields using this function (Figure 6.7) demonstrated that it was appropriate but that even when it was used observed RUE was lower (~0.5) than expected during the initial crop phases (< 10 fully expanded leaves). Further experimentation may elucidate the mechanism behind this result. The process of creating, modifying and testing these hypotheses has uncovered some of the driving factors behind RUE in *Zea mays*.

The next step with the current data would be to link it to a balanced simulation of P uptake e.g APSIM P (Probert, 2004) or DSSAT (Daroub *et al.*, 2003). This would form a powerful analytical tool to test hypotheses of crop responses to P. In such a model it may also be possible to simulate aspects of sweet corn quality such as individual kernel mass and unfilled tip length using a source limited approach both when kernel number is set (around silking) and during kernel filling (post silking). Testing this model in diverse environments may indicate where current understanding is inadequate or where assumptions made in this thesis are too simplistic. One such assumption is probably that HI is constant across experimental

data sets. A more logical approach would be to include a linear rate of increase of HI (e.g. Muchow *et al.*, 1990).

8.6 Opportunities for further research

Apart from these modelling applications, other aspects of crop growth outlined in this thesis warrant further investigation.

8.6.1 Mechanism by which P deficiency limits individual leaf area

1. The mechanism by which P supply limits leaf area in field grown *Zea mays* is not well understood. An experiment where maize grown initially in a P deficient environment was transferred to an excess P supply at each of leaf stages 1-10 could increase this understanding. A break in the leaf area distributions of these plants would indicate that the area of individual leaves was limited by current P supply. The theoretical response in Figure 8.2 is for a plant transferred at the 10 leaf stage. However, similar responses would be expected for plants transferred between P treatments at other leaf stages. In contrast, if the leaf area distribution showed no response to a replenishment of P supply this would indicate that the area of the lower leaves may have limited the area of the upper leaves via its effect on cell expansion independent of the current P supply.

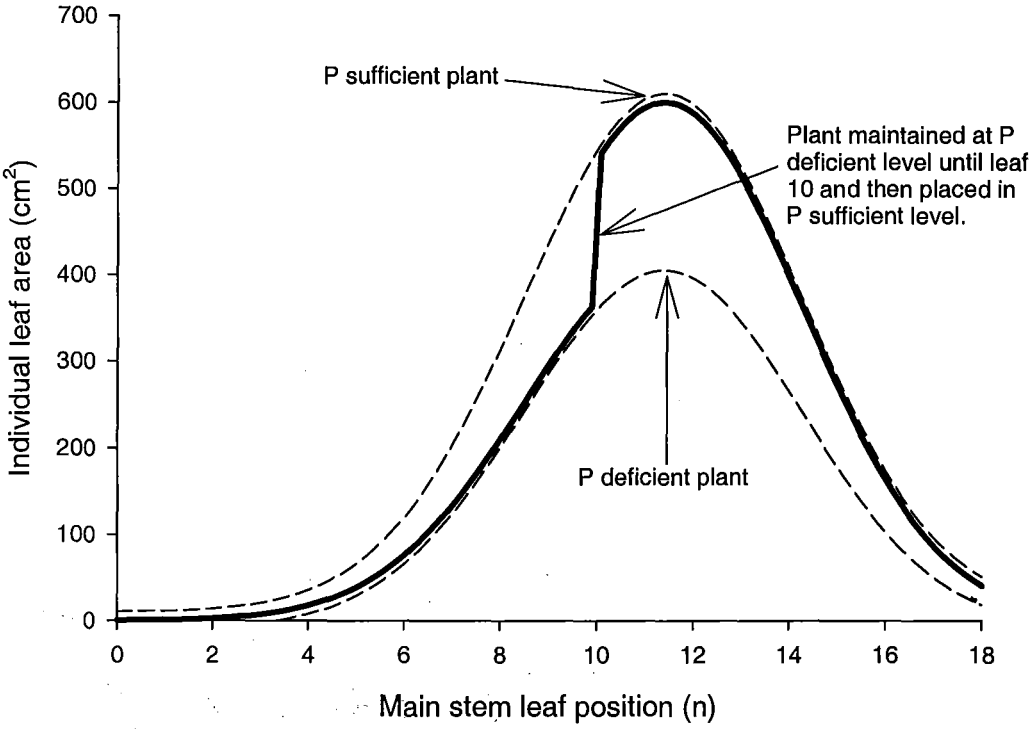

Figure 8.2 Theoretical response of *Zea mays* leaf area distributions for plants grown under either P deficient, P sufficient or P deficient until appearance of leaf 10 and then P sufficient conditions. The theoretical response which would indicate that the area of leaves ≥11 were not limited by the area of leaves ≤10, is represented by the solid line.

2. The potential source limitation on individual leaf area could also be examined using a defoliation experiment similar to that of Johnson (1978). If the reduced leaf areas and leaf appearance rates in response to limited P supply could be replicated by defoliation treatments it would indicate that a source limitation may be the cause.

3. A re-analysis of photosynthetic response to P and the interaction with leaf position is required. This should focus on measurements of photosynthesis at 2000 μmol PPFD m^{-2} s^{-1} and not measure full light curves. It would also be enlightening to measure leaf photosynthesis down through the canopy to examine the extent to which P remobilisation affects photosynthetic rates. These results could then be used to simulate (e.g. Rodriguez *et al.*, 1998b) the potential source limitation on leaf area in P deficient sweet corn.

8.6.2 Low RUE during establishment

1. A further examination of the low RUE during maize establishment (Figure 6.1) could use a multi-location factorial experiment with sowing dates (to manipulate development and solar radiation) and plant populations (to manipulate GLAI) as the treatments. Solar radiation interception would need to be accurately measured in each plot using logging tube solarimeters to eliminate errors in RI_{cum}.

2. An examination of growth partitioning between roots and shoots for the duration of a maize crop may isolate a mechanism causing this low RUE during establishment.

8.7 Conclusions

'Challenger' sweet corn crops grown with a limited P supply had less RI_{cum} and hence less total crop DM. Specific findings of the results chapters were:

- **Chapter 4.** 'Challenger' sweet corn grown without P fertiliser produced less total crop DM, but this was conservatively partitioned into each of its components. Kernel DM made up 24% of crop DM at canning maturity regardless of N or P fertiliser treatment. Consequently, kernel yield decline was directly proportional to crop DM decline under a limited P supply.

- **Chapter 5.** 'Challenger' sweet corn grown without P fertiliser intercepted ~200 MJ m^{-2} less solar radiation than P fertilised crops, due to both a decreased individual leaf area and a reduced rate of leaf tip and fully expanded leaf appearance.

- **Chapter 6.** P fertiliser did not alter RUE in 'Challenger' sweet corn. RUE followed a consistent temperature function (Wilson *et al.*, 1995), but was about half that expected at early crop development stages. RUE was 0.66 g MJ^{-1} before the full expansion of leaf 10 and 1.34 g MJ^{-1} subsequently.

- **Chapter 7.** Simple simulation analyses showed that a single asymptotic response curve to P was inappropriate for multiple sites and seasons. The risk of 'Challenger' sweet corn failing to mature before the first autumn frost increased by ~10% without P fertiliser in Canterbury.

This thesis provides a step towards a semi-mechanistic model of sweet corn growth and development responses to P. These data, when linked to a balanced model of P uptake would

form a powerful analytical tool. Development and testing of such a model would highlight further gaps in knowledge and guide further research.

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Appendices

Appendix 1 Selected references where T_b has been determined for various periods in sweet corn and grain maize.

Location(s)	Seasons	Sowing dates	HYB	*Method*	T_b *(°C)*	*Phase*	*Reference*
			Sweet corn				
Feilding Gisborne Hastings (NZ)	5 10 4	Factory Record	4 3 4	RE+ CV	**6**	E-M	(Brooking and McPherson, 1989)
Lincoln Ashburton (NZ)	2 1	6 3	3† 3†	RE	**6-8**	E-M	(Wilson and Salinger, 1994)
Bundaberg Gatton QLD (AUS)	1 1	4 14	9 9	DEV	**5.4-6.4**	E-M	(Olsen *et al.*, 1993)
Tennessee (USA)	1	8	1	SD‡ ST CV RE	**5.4** **10.4** **6.4** **6.3**	E-M	(Yang *et al.*, 1995)
			Maize				
24 locations 18 countries	5	53*	18	CV	**6**	E-S	(Bonhomme *et al.*, 1994)
Gatton QLD (AUS)	1	7	5	DEV	**8**	E-TI	(Birch *et al.*, 1998a)
Katherine NT (AUS)	1	5	1	RE	**0**	S-M	(Muchow, 1990)
8 European countries	3		11	CV	**7-9**	E-S	(Derieux and Bonhomme, 1982a)
9 European countries	3		11	CV	**4-8 #(6)**	S-M	(Derieux and Bonhomme, 1982b)
Wageningen (Netherlands)	1	5	3	DEV	**8**	E-S	(Birch, 2003)
Controlled environment	16 temps		12	RE	**8.4-10.2**	E-TI	(Ellis *et al.*, 1992)
Controlled environment	18 temps		2	RE	**7**	E-S	(Warrington and Kanemasu, 1983)

† One hybrid was sown on one date in each season only. ‡ Compared 4 methods of evaluating T_b. * 53 location by sowing date combinations. # 6 was obtained most often.

Data are sorted according to crop type (sweet corn and maize), locations, seasons, sowing dates, number of hybrids tested (HYB), method used to determine Tb (CV is coefficient of

variation in Tt method, RE regression method, SD standard deviation in days method, ST standard deviation in Tt method, and DEV using DEVEL optimizations program (Holzworth and Hammer, 1992)), and period studied (E-M, emergence to maturity; E-S, emergence to silking; S-M, silking to maturity; and E-TI, emergence to tassel initiation).

Appendix 2 Soil test data taken after Experiments 1 and 4.

Soil test P values are reported for each treatment and the status of other nutrients is reported for the whole experiment.

Soil test P values for Experiment 1 (17 June 2002).

kg P ha^{-1} applied	*Mean Olsen P value ($\mu g\ ml^{-1}$)*	*ppm soil*
0	5	6
50	10	11
100	14	15
150	17	19
200	35	39

Common soil test for other nutrients in Experiment 1 (17 June 2002).

Nutrient	*pH*	*K*	*S* SO_4	*Mg*	*Ca*	*Na*
Unit	-	MAF QT	ppm	MAF QT	MAF QT	MAF QT
Soil test value	4.9	4	4	8	4	3
ppm soil	-	80	-	40	500	15

Soil test P values for Experiment 3 (14 May 2003).

kg P ha^{-1} applied	*Mean Olsen P value (µg ml^{-1})*	*ppm soil*
0	10	11
50	16	18
110	24	27
170	32	36
240	36	40

Common soil test for other nutrients in Experiment 3 (14 May 2003).

Nutrient	*pH*	*K*	*S*	*Mg*	*Ca*	*Na*
			SO_4			
Unit	-	MAF QT	ppm	MAF QT	MAF QT	MAF QT
Soil test value	5.7	7	4	7	5	4
ppm soil	-	140	-	35	625	20

Appendix 3 Plant populations and variation in plant populations for Experiments 1, 3 and 4.

Plant populations were estimated for Experiments 1, 4 and 5. The mean distance (mm) between 50 plants in Experiment 1 and 20 plants in Experiments 3 and 4 were measured from each plot. This data was used to calculate the mean population for each plot and a CV% to quantify any intra plot variation. These values were tested using ANOVA (Section 3.8) and are presented below. There were no differences in mean plant population or in CV% in any experiments.

Mean plant population and variation in plant spacing for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in Experiment 1 (2001/2002).

Treatment	*Plants ha^{-1}*	*CV (%)*
P0	54849	26.3
P50	63910	23.2
P100	53598	27.4
P150	55973	25.7
P200	65665	22.5
α Value	0.619	0.668
Grand mean	58799	25.0

Mean plant population and variation in plant spacing for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in Experiment 3 (2002/2003).

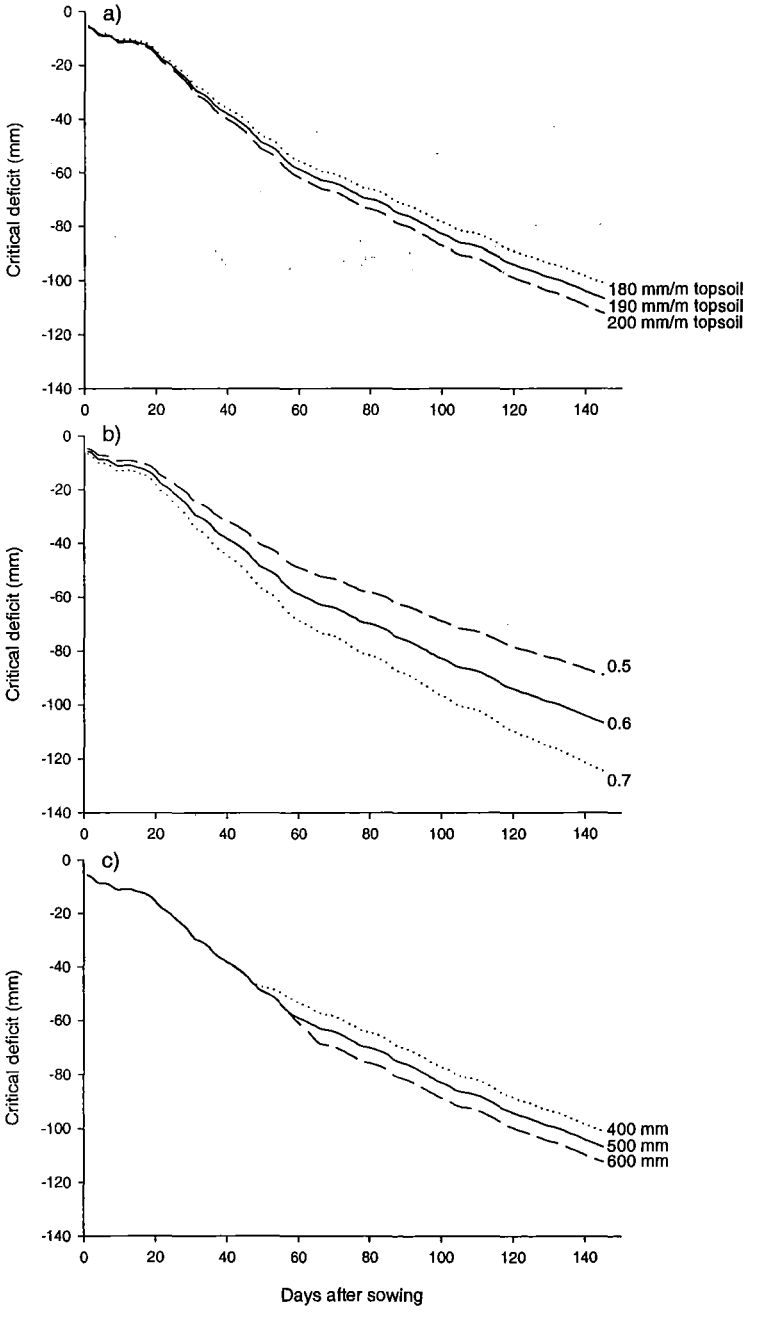
Treatment	*Plants ha^{-1}*	*CV (%)*
P0	56449	22.3
P50	57145	19.6
P110	56716	27.3
P170	54960	24.6
P240	58136	21.3
α Value	0.971	0.949
Grand mean	56681	23.0

Mean plant population and variation in plant spacing for 'Challenger' sweet corn grown in Lincoln, Canterbury, New Zealand in Experiment 4 (2002/2003).

Treatment	*Plants ha^{-1}*	*CV (%)*
P240	56736	17.9
P260	51348	34.3
P280	57500	24.4
P320	53490	36.2
P380	52954	30.8
α Value	0.620	0.271
Grand mean	54406	28.7

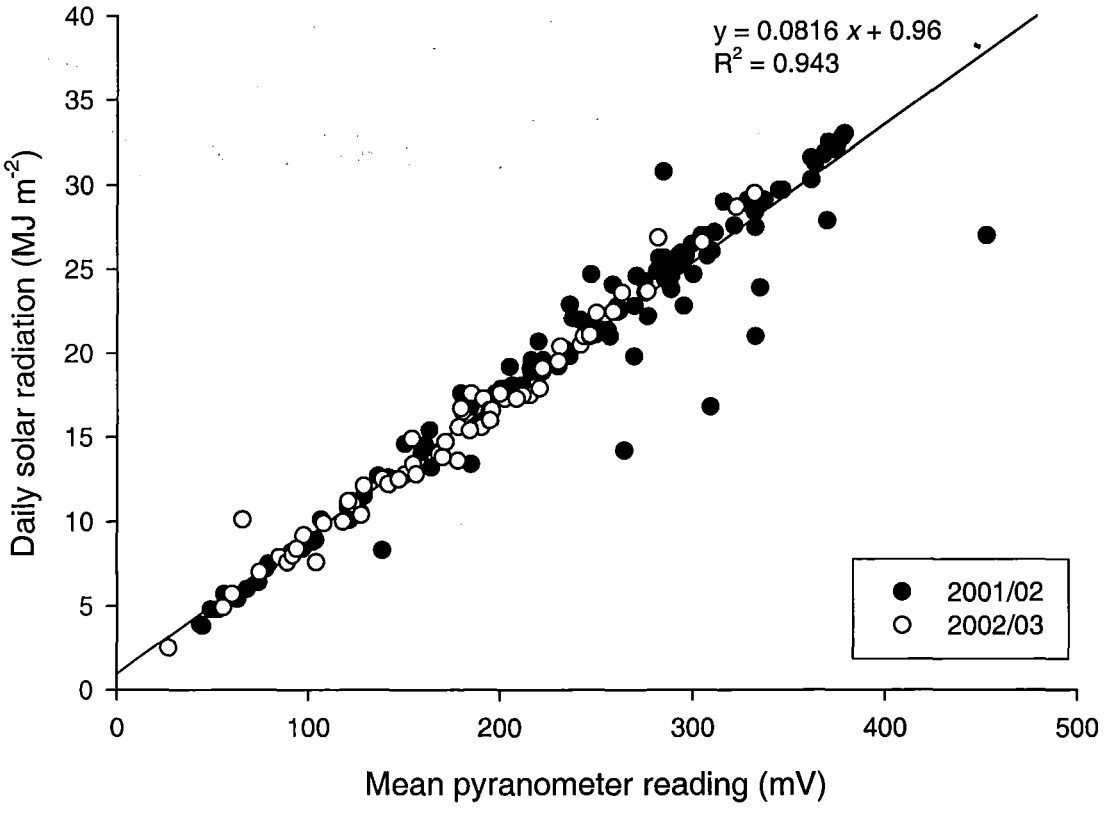
Appendix 4 Sensitivity of calculated D_c to assumed variables used in Section 3.6.1.1.

The sensitivity of calculated Dc to variations in a) total AWC per metre of top soil (180, 190 and 200 mm AWC m^{-1} topsoil); b) the fraction of AWC that was plant available (0.5, 0.6, and 0.7); and c) the soil depth to stones (400, 500, and 600 mm) were examined using the weather data and sowing dates from the 2002/03 season.

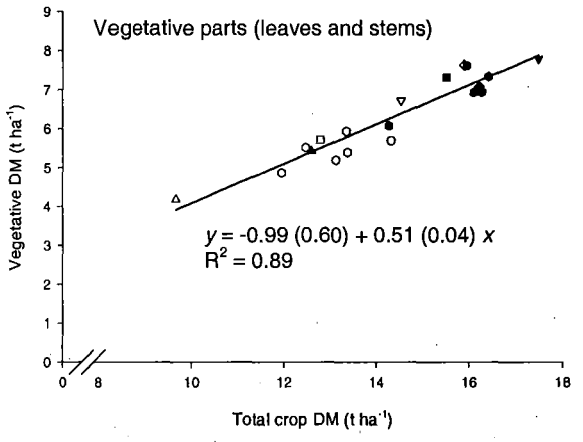


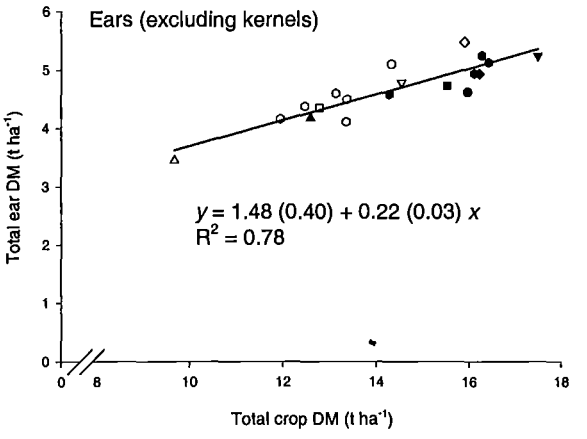
Appendix 5 Linear regression between daily incident solar radiation measured at Broadfields' meteorological station MJ m^{-2} and mean daily pyranometer reading (mV) above the experimental site (Section 3.7.6.2) for both 2001/02 and 2002/03.

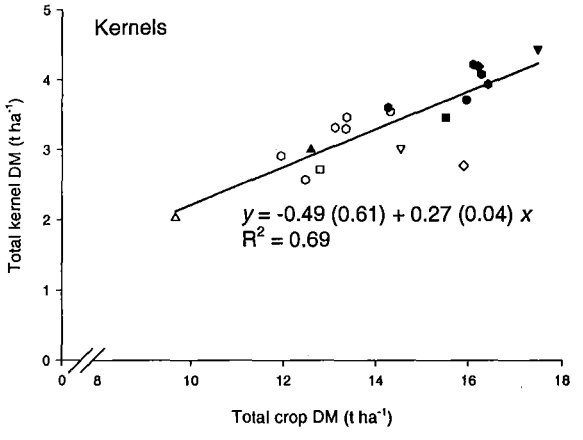
The data sets were incomplete due to a malfunction of the data logger and therefore only those measurements for those days were used.



Appendix 6 Regressions for biomass partitioning (Section 4.3.2).







These regressions were not constrained to pass through the origin. In the regressions the values in parentheses represent the standard errors of each variable. The symbols and treatments are in Table 4.1

Appendix 7 Measured kernel moisture at final harvest in experiments 1, 2, 4 and 5.

2001/02		*2002/03*	
Treatment	Measured kernel moisture (%)	Treatment	Measured kernel moisture (%)
	Experiment 1		Experiment 3
0 kg P ha^{-1}	75.2	0 kg P ha^{-1}	73.0
50 kg P ha^{-1}	76.6	50 kg P ha^{-1}	74.9
100 kg P ha^{-1}	74.7	110 kg P ha^{-1}	74.9
150 kg P ha^{-1}	75.6	170 kg P ha^{-1}	73.8
200 kg P ha^{-1}	76.6	240 kg P ha^{-1}	73.7
	Experiment 2		Experiment 4
0 kg N ha^{-1}	76.6	240 kg P ha^{-1}	74.3
45 kg N ha^{-1}	74.1	260 kg P ha^{-1}	73.5
90 kg N ha^{-1}	74.9	280 kg P ha^{-1}	74.7
180 kg N ha^{-1}	74.6	320 kg P ha^{-1}	73.9
300 kg N ha^{-1}	74.8	360 kg P ha^{-1}	74.2

Appendix 8 Derivation of appropriate Tb's for quantifying Tt for the periods between emergence to silking and silking to harvest maturity.

Analysis:

The analysis in this appendix uses data from a third experiment sown in 2001/02. This experiment used three sowing dates (18 October, 8 November and 15 November 2001) in a completely randomised design. Basal dressings of CAN, TSP and PS were applied (Section 3.3.1) to all of these 4.9m wide (7 rows) and 5 m long (24.5 m^2).

Data for both date of silking and date of maturity (Section 3.7.4) from this experiment and also the 200 kg P ha^{-1} crop in experiment 1 and the 300 kg N ha^{-1} crop in experiment 2 were used to examine the most appropriate T_b for Tt calculations in Chapter 4. Thus, there were 5 sowing dates in total used for analysis. Before analysis the date of maturity was corrected for kernel moisture content using the method outlined in Section 4.2.2.4. These corrected maturity dates were then used in subsequent analyses.

A range of T_b from 10-15 °C, in 1 °C steps, were tested for each of the emergence to silking and silking to maturity periods, and a separate Tb was calculated for each. For each T_b the Tt between either emergence and silking or silking and maturity was calculated using the modified sine curve method outlined in Section 2.5.1. These durations were calculated separately for each plot and then the mean Tt and the standard deviation were used to calculate the coefficient of variation (CV%) in Tt for each T_b. The lowest CV% was then used as the criterion to select the most appropriate T_b for quantifying phenological development.

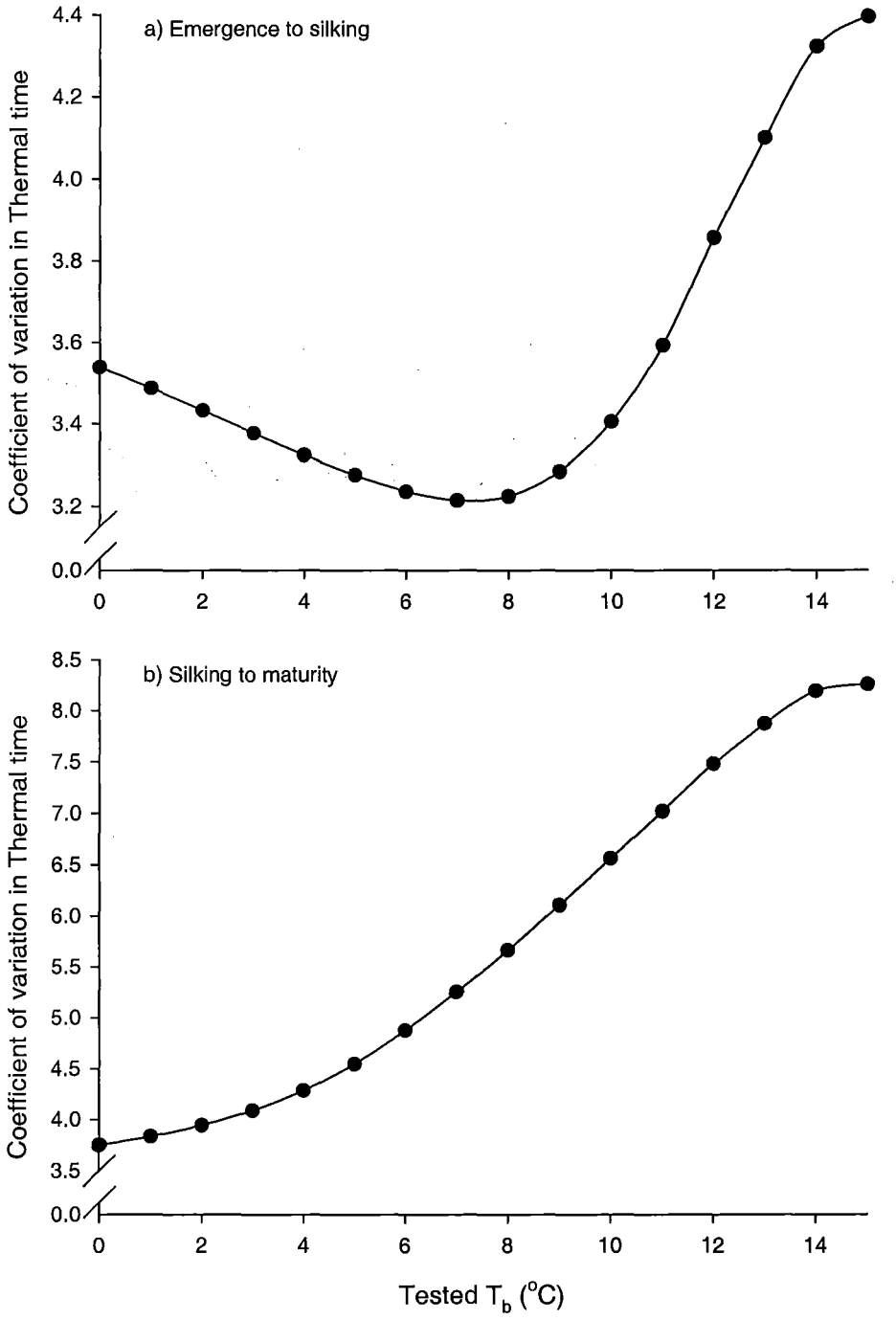


Figure A.1. The effect of a range of T_b's (0-15 °C) on the coefficient of variation in calculated Tt between (a) emergence and silking, and (b) silking and maturity in Experiments 1,2 and 3.

Results and Discussion:

The lowest CV% for the emergence to silking period was found at 7 °C (Figure A.1 a). However, there was only a minor increase in CV% if T_b= 8°C was used. A T_b of 8°C is consistent with the literature (Birch, 2003; Derieux and Bonhomme, 1982a; Muchow *et al.*, 1990). Therefore T_b= 8°C was selected as the most appropriate Tb for the period and used for the analyses in Chapter 4.

The lowest CV% for the silking to maturity period was found with a T_b of 0°C (Figure A.1 b). There was a steady increase in CV% as T_b was increased above 0°C. This is also consistent with the literature for maize (Muchow, 1990) and so was used for the analyses in Chapter 4.

When a single T_b was used for both periods (i.e. emergence to maturity) the lowest RMSD was found at a T_b of 15°C (Data not shown). This is much greater than any value in the literature and is substantially higher than either T_b found for either the emergence to silking or silking to maturity periods derived independently. This indicates that the T_b's for the separate periods were mutually compensating and that using a separate T_b for both periods was most appropriate.

Appendix 9 P concentration and uptake of P for individual biomass components, and total uptake of P at final harvest for 'Challenger' sweet corn grown at Lincoln, Canterbury, New Zealand in Experiments 1 and 4.

Total P uptake (kg P ha^{-1}) and P yield of individual DM components of 'Challenger' sweet corn crops from Experiments 1 and 4. The values in parentheses indicate the percentage of total P uptake in that DM component.

P applied kg P ha^{-1}	*Total (kg P ha^{-1})*	*Kernel (kg P ha^{-1})*	*Husk leaves (kg P ha^{-1})*	*Rachis (kg P ha^{-1})*	*Leaves (kg P ha^{-1})*	*Stems (kg P ha^{-1})*
2001/02						
0	15.3	6.8 (44%)	1.2 (8%)	3.2 (21%)	2.3 (15%)	1.9 (12%)
50	24.1	11.6 (48%)	2.3 (9%)	4.1 (17%)	3.7 (15%)	2.5 (10%)
100	28.1	14.1 (50%)	2.7 (10%)	5.0 (18%)	3.6 (13%)	2.7 (10%)
150	25.5	11.8 (46%)	1.8 (7%)	5.1 (20%)	3.9 (15%)	2.8 (11%)
200	29.0	11.2 (39%)	2.9 (10%)	6.4 (22%)	5.0 (17%)	3.5 (12%)
2002/03						
0	23.1	13.1 (56%)	1.3 (6%)	4.1 (18%)	2.9 (13%)	1.8 (8%)
50	29.7	13.9 (47%)	2.1 (7%)	5.4 (18%)	5.7 (19%)	2.7 (9%)
110	23.7	9.5 (40%)	1.8 (7%)	3.8 (16%)	2.6 (24%)	3.1 (13%)
170	32.7	17.2 (52%)	1.5 (5%)	5.7 (17%)	5.1 (16%)	3.2 (10%)
240	29.7	13.1 (44%)	2.0 (7%)	4.7 (16%)	6.3 (21%)	3.7 (12%)

P concentration (%) of individual biomass components for 'Challenger' sweet corn grown in Experiments 1 and 4.

P applied kg P ha^{-1}	*Kernel*	*Husk leaves*	*Rachis*	*Leaves*	*Stems*
2001/02					
0	0.36	0.09	0.17	0.18	0.07
50	0.41	0.12	0.16	0.20	0.07
100	0.38	0.12	0.17	0.19	0.07
150	0.41	0.1	0.20	0.18	0.07
200	0.42	0.14	0.21	0.19	0.08
2002/03					
0	0.34	0.07	0.16	0.18	0.06
50	0.37	0.09	0.19	0.22	0.06
110	0.39	0.09	0.15	0.22	0.06
170	0.38	0.07	0.19	0.19	0.06
240	0.37	0.11	0.18	0.26	0.08

Appendix 10 Relationships between leaf areas measured for photosynthetic measurements and for leaf area distributions

The area of individual leaves measured using the Licor 3100 leaf area meter in Section 3.7.1.2 was plotted against the area of the leaves used for photosynthesis measurements in Section 6.2.2.2. The areas of individual leaves were combined for each leaf position of each treatment. The relationship between the two measurements was examined using least squares regression. In 2001/02 there was close agreement between the two measurements (Figure A.2 a). In contrast the individual area of the leaves used for the measurement of photosynthesis (Section 6.2.2.2) was 25% greater than that found for the leaves measured in Section 3.7.1.2. Thus, the area of individual leaves in 2002/03 was corrected using this regression before their statistical analysis in Chapter 5, while the area of individual leaves in 2001/02 was unchanged.

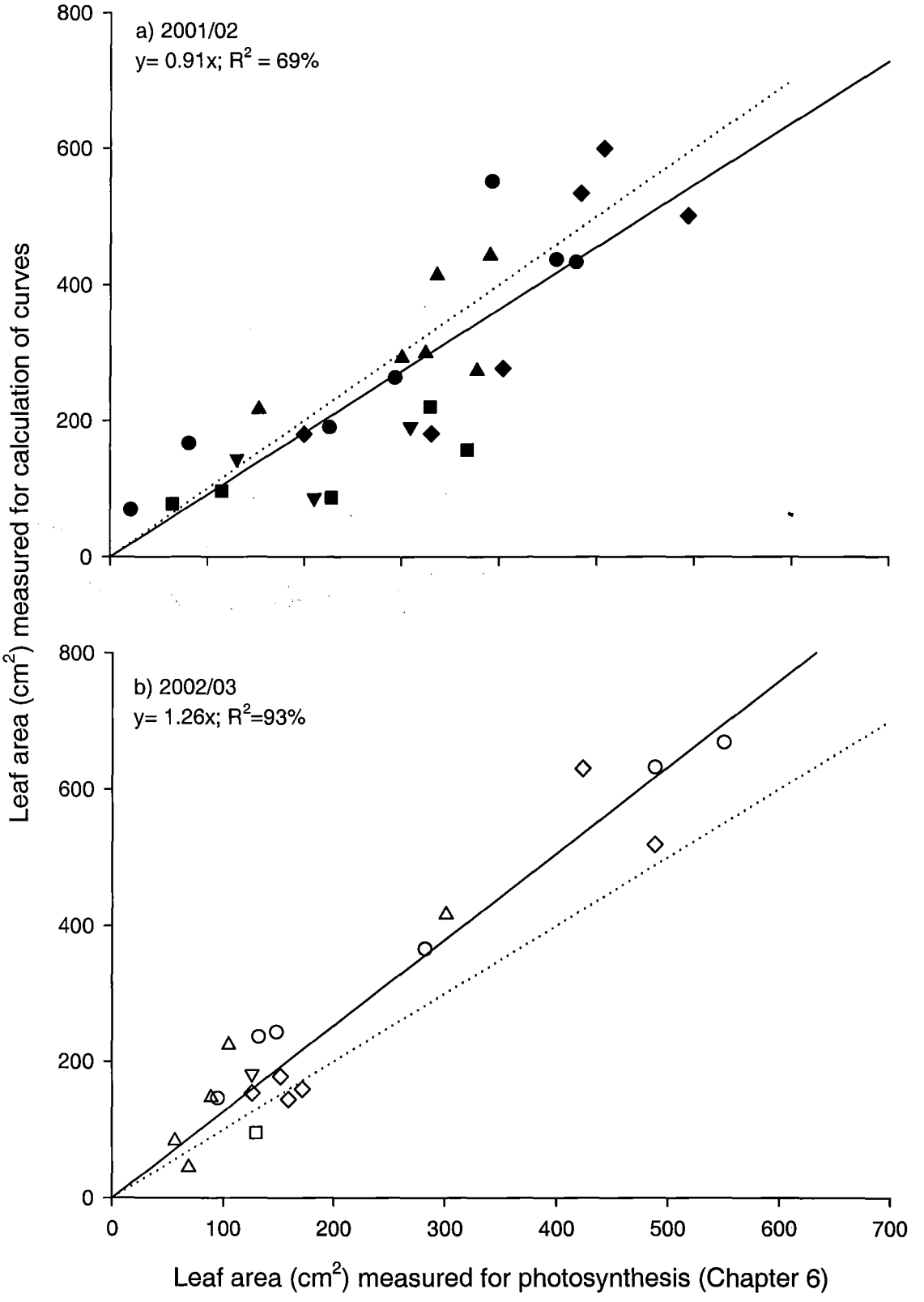
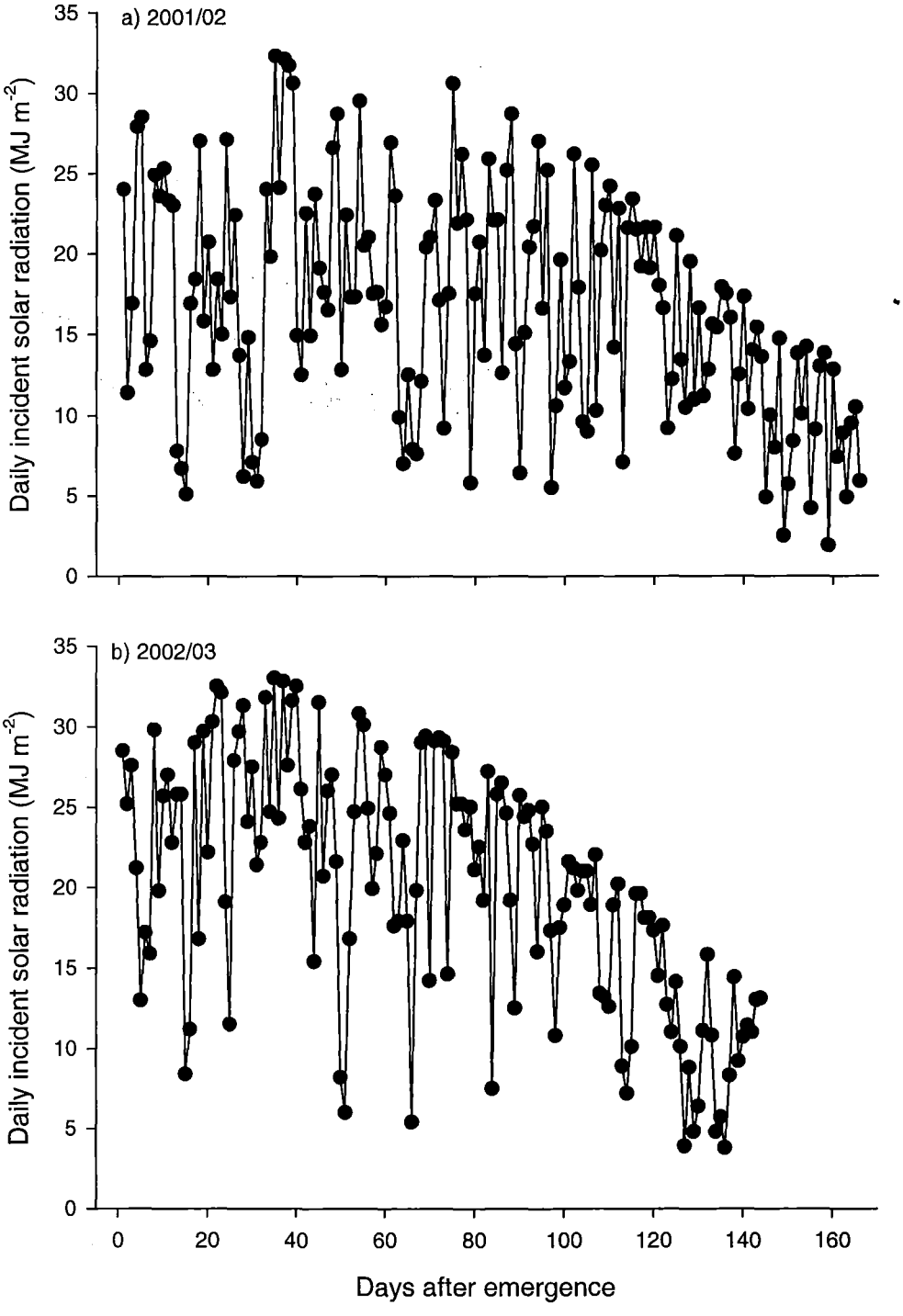


Figure A.2. Relationship between the areas of individual 'Challenger' sweet corn leaves measured to determine leaf area distributions in Chapter 5 plotted against the area of those leaves used for photosynthetic measurements in Chapter 6 for (a) 2001/02 and (b) 2002/03. The solid lines are the regressions and the dotted lines are the 1:1 relationship. Both measurements were made using the Licor 3100 leaf area meter. Symbols in Table 4.1

Appendix 11 Measured values of daily incident solar radiation (MJ m^{-2}) measured at Broadfields' meteorological station in 2001/02 and 2002/03.



Appendix 12 Calculated Radiation use efficiencies for the different P treatments using a single straight line regression for each plot.

Treatment kg P ha^{-1}	*RUE (g DM MJ^{-1})*
2001/02	
0	0.96
50	1.2
100	1.2
150	1.2
200	1.3
s.e.	0.073
2002/03	
0	1.23
50	1.25
110	1.16
170	1.12
240	1.32
s.e.	0.565

s.e. is the pooled standard error of the treatment means.

List of publications

Fletcher, A. Moot, D. and Stone, P. 2003. Canopy development in phosphorus deficient sweet corn. In "Solutions for a better environment". Proceedings of the 11th Australian Agronomy Conference, 2- 6 Feb 2003, Deakin University, Geelong, Victoria, Australia.

Fletcher, A. Moot, D.J. and Stone, P. 2003. Fertiliser P effects on biomass partitioning and quality of sweet corn in a cool temperate environment. In "New directions for a diverse planet". Proceedings for the 4th International Crop Science Congress, Brisbane, Australia, 26 September- 1 October 2004.

Fletcher, A.L. and Moot, D.J. 2003. Sowing date and fertiliser effects on sweet corn phenological development. *Proceedings Annual Conference Agronomy Society of New Zealand* **33**:35-42.

Fletcher, A.L., Moot, D.J. and Scott, W.R. 2004. Leaf appearance and primordia initiation of 'Challenger' sweet corn in response to phosphorus. *Proceedings Annual Conference Agronomy Society of New Zealand* **34**:89-96.

Fletcher, A.L., Moot, D.J. and Stone, P.J. 2002. Canopy development of sweet corn in response to phosphorus. *Proceedings Annual Conference Agronomy Society of New Zealand* **32**:7-15.

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